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A REVISION OF THE SMELT FAMILY, OSMERIDAE

By

D. E. McALLISTER

DEPARTMENT OF NORTHERN AFFAIRS AND NATIONAL RESOURCES
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D. E. McALLISTER

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DEPARTMENT OF NORTHERN AFFAIRS AND NATIONAL RESOURCES
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A REVISON OF THE SMELT FAMILY, OSMERIDAE

INTRODUCTION

The smelts, family Osmeridae, are small salmonoid fishes inhabiting the waters of the northern hemisphere. Their white, delicately flavoured flesh, their aggregating tendency, and their ease of capture make them of economic importance, an economic importance which is, as yet, only partially realized. Despite this, they have been poorly studied taxonomically. Because of the lack of world-wide studies, the taxonomic status accorded to taxons has been variable.

The following are major papers on smelt systematics. The first is that of Hubbs (1925). In it, generic relationships were clarified, the species were allotted to the genera in which they now stand, and keys to the genera and species were presented. The second is that of Chapman (1941), on the osteology of the Osmeridae. Chapman compared the skulls of one species from each genus and commented on the relationships of the family. Further, the problematical *Therebromus callorhini* Lucas, from fur seal stomachs, was discharged from the family. Hamanda (1954, 1957, 1961) first discovered that there were three species of *Hypomesus* and made a major contribution to their biology. Hubbs and Chapman (1951) placed in synonymy two nominal species of osmerids based on larvae. Gosline, in a classification of the modern Isospondyli (Clupeiformes), and Norden (1961), in a study of the osteology of the Salmonoidei, made comments on the Osmeridae. Okada (1960) described, illustrated, and summarized the literature on Japanese species, Hart and McHugh (1944) on British Columbia species. The author has a manuscript bibliography with over seven hundred titles.

This study is a systematic revision of the family Osmeridae. It presents synonymies, descriptions, and keys to subfamilies, genera, species, and subspecies. Sketches and spot distribution maps are given for each species. Previous to this study some fourteen to sixteen species were recognized. In this paper ten species are recognized. There are thirteen forms counting species and subspecies. Generic limits are unchanged. Two subfamilies are established. A new species with a new subspecies is named.

Methods

Measurements were made with 200 mm dial calipers reading to 0.1 mm. Except for the pectoral/pectoral to pelvic proportion, ratios of body parts were determined directly using needle-point dividers. Standard length was taken from the anteriormost tip of the body, the tip of the lower jaw with the mouth closed, to the caudal flexure. Head length was taken to the posterior bony edge of the operculum; orbital diameter horizontally between the fleshy rims of the orbit. Pectoral length was taken from the dorsal point of insertion to the posterior tip; adipose base, the length of the portion adhering to the body; adipose length between the anterior insertion and the posterior tip; the longest anal ray from its base to its tip; the pectoral-pelvic distance was measured between the dorsal insertions of these fins. The body depth was taken at its deepest point. The interorbital width was measured as the narrowest fleshy distance.

Counts were made under a mono-objective binocular microscope. Only rays reaching the distal edge of the dorsal and anal fins (primary rays) were counted. The last two rays of these fins, which were usually closely adjoined at the base, were counted as one. The caudal ray count included only the primary rays, i.e., the branched rays plus two large unbranched rays, one of which is above and one below the branched rays. All rays were counted in the paired fins. Only pored scales were counted in the lateral line; when complete they were counted to the caudal flexure. When the lateral line was incomplete, as it is in most osmerids, a midlateral scale count was made. This count includes the pored scales and the scales along the midline of the side that would have been pierced had the lateral line been complete to the caudal flexure. Vertebral counts, made from X-ray plates, include the single upturned urostyle vertebra at the end of the column. Branchiostegal, scale, paired fin ray, gill-raker counts, and measurements were made on the left side. The gill-rakers of the first arch are presented as the number on the upper limb plus the number on the lower limb (including the one in the fork of the two limbs) equalling the total number of gill-rakers, in this way; 10–13+21–24=31–36. Even the smallest rakers were included. The smallest evaginations were counted in pyloric caeca enumerations.

Where dependable counts or measurements were found in the literature, outside the range of those personally examined, the author's ranges were augmented. Rare counts or measurements are included in parentheses, P 14–16(17), rare meaning about 5 per cent or less.

The sketches of the fish were made employing a camera lucida. The spot distribution maps were compiled from literature and museum records. They do not present every literature record, except in some of the rarer species, but they do give a general outline of distribution with more emphasis toward the limits of ranges. As each spot covers a considerable area, more than one record may be spanned by a single spot.

ARRANGEMENT

The species accounts are organized in the same fashion under synonymy, diagnosis, description (meristics, proportions, structure, colour, size), sex dimorphism, life-history, taxonomy (not always present), and material examined. The synonymy cites only new names, not later identifications. The illustration for each species includes an inset of the dentition and one of the intestines showing the pyloric caeca, stomach form, and the attachment of the ductus pneumaticus to the gas bladder.

ABBREVIATIONS

The following abbreviations are used:

NMC — National Museum of Canada
BC — Institute of Fisheries, University of British Columbia
ROM — Royal Ontario Museum
UMMZ — University of Michigan Museum of Zoology

CAS — California Academy of Sciences
OSC — Dept. Fisheries, Oregon State College
UW — College of Fisheries, University of Washington
D — dorsal fin rays
C — caudal fin rays
A — anal fin rays
V — ventral fin rays
P — pectoral fin rays
L.L. — pored scales in lateral line

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The author is deeply indebted to Dr. J. C. Briggs, under whose guidance this study took place and who permitted use of his fine library. Dr. K. Hamanda of Hokkaido University, Dr. George A. Allen of Humbolt State College, California, Dr. A. B. Albrecht of California Department of Fish and Game, Dr. R. M. Bailey of the University of Michigan, Dr. W. I. Follett of the California Academy of Sciences, Dr. G. S. Myers of Stanford University, Dr. E. C. Raney of Cornell University, Dr. W. Templeman of Fisheries Research Board, Newfoundland, and Dr. A. D. Welander of the University of Washington kindly donated or loaned specimens. Dr. C. C. Lindsey of the Institute of Fisheries helped in the selection of common names, made criticisms, and permitted use of X-ray equipment. Dr. N. J. Wilimovsky of the Institute of Fisheries permitted examination of his Alaskan collections and use of rare Arctic publications from his library. He also checked the manuscript. Mr. R. Dryfoos of the University of Washington permitted examination of his new records of *Spirinchus* from Alaska. Mr. G. F. Hartman sent specimens of smelt from Sweden, Dr. G. H. Allan from California, and Mr. M. Yesaki from Vancouver.

Mr. T. Ueno found and translated numerous Japanese papers on Osmeridae. Mr. J. G. Hunter provided several records of smelts from the Canadian Arctic. Mr. J. D. McPhail checked literature at McGill University and made several suggestions. Dr. E. J. Crossman generously checked characters on specimens of *Osmerus eperlanus mordax* at the Royal Ontario Museum. Mr. F. Cook sent material from the National Museum of Canada. Dr. Robert Kanazawa of the U.S. National Museum provided an X-ray. My wife, Nancy A. McAllister, kindly translated a German paper. Dr. E. L. Bousfield identified invertebrate stomach contents.

Dr. Wann Langston, Jr. of the National Museum of Canada, Dr. Donald Baird of Princeton University, Dr. Theodore H. Eaton, Jr. of the University of Kansas, and Dr. Nelson R. Gadd of the Geological Survey of Canada aided me with fossils.

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Permission was kindly granted by the Department of Geography, University of Chicago, to use their Goode Base Map 201 PN, copyright by the University of Chicago.

SYSTEMATIC SECTION

Suborder SALMONOIDEI

Superfamily *OSMEROIDEA*

Family OSMERIDAE—THE SMELTS

Synonymy

Salmone Risso 1810, p. 322 (*ex parte*).

Salmones Cuvier 1817, p. 159 (*ex parte*).

Osmerus Faber 1829, p. 174 (misprinted *Osmarus*).

Salmonidae Bonaparte 1831, p. 115 (*ex parte*).

Microstomidae Gill 1872, p. 16 (*ex parte*).

Argentinidae Gill 1893, p. 112 (*ex parte;* ex Argentininae Gill 1863).

Osmeridae Regan 1913, p. 290 (type genus: *Osmerus* Linnaeus by Direction 69 of the International Commission on Zoological Nomenclature).

Elegant, small, tasty, silvery fishes under 300 mm (a foot) in standard length. Many with a curious cucumber odour. Feed on small invertebrates and fishes. Eggs demersal, adherent. Dwell in the boreal and subarctic waters of the northern hemisphere, in lakes, streams, and marine shelf waters, above the bottom.

Supramaxillary, mesocoracoid, and proethmoid(s) present. No intramuscular bones, post-terminal vertebral centra, median shaft on vomer, orbitosphenoid, nor basisphenoid. Vomer single.[1] Teeth on mesopterygoid, glossohyal, vomer, palatines, premaxillary, maxillary, dentary, basibranchial plate teeth (may be lost in spawning *Thaleichthys*). Teeth on pterygoid and ceratobranchial of 5th gill arch absent. Vertebrae 51 to 78 (including last upturned urostylic centrum). Only the last vertebra is turned up. Posterior neural and haemal spines with anteroposteriorly oriented blades. Myodome opening posteriorly. Branchiostegals 6 to 10, the upper ones spathiform. Pyloric caeca 0 to 11. Stomach with blind sac (except in *Hypomesus* and *Spirinchus* where reduced or absent). No discernible ringfalten in intestine. Gill membranes separate. Pseudobranch present. Pelvics abdominal and lacking axillary appendage. Lateral line present but usually incomplete. Nineteen principal caudal rays, 17 branched. Ventral rays 8 (plus one small ray in *Mallotus*). Adipose present.

The Osmeridae includes 2 subfamilies, 6 genera, 10 species, and 13 forms counting monotypic species and subspecies. They are marine, anadromous, or landlocked and freshwater, in the Pacific, Arctic, and Atlantic oceans and their drainages, in the northern hemisphere. The total distribution is depicted in Figure 1.

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[1] Contrary to Chapman (1941), the vomer was found unpaired in an adult *Osmerus* from Pacific and one from Atlantic America. It might be paired in young, however.

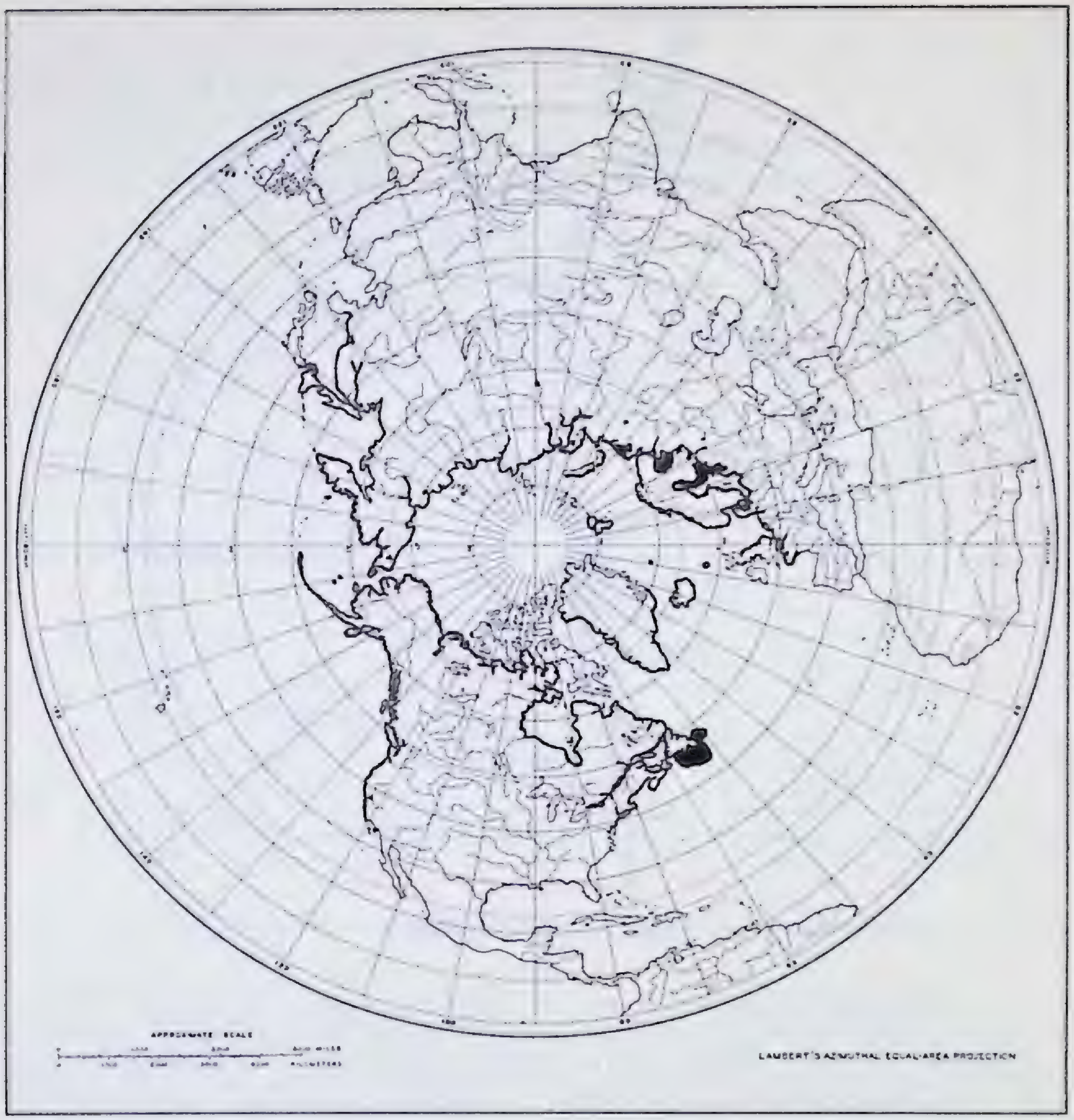


FIGURE 1. Distribution of the smelt family, Osmeridae. Some small distributional gaps are bridged. (The eastern Pacific question mark is an uncertain record of *Allosmerus*.)

RELATIONSHIPS

The relationships of the Clupeiformes (Isospondyli) have recently been investigated by Gosline (1960). Gosline places the Osmeridae in the superfamily Osmeroidae, which in turn belongs to the Suborder Salmonoidei adjacent to the Suborder Esocoidei. The phylogenetic relationships of the Osmeridae are depicted in Figure 2, modified slightly from Gosline.

Although some authors have reduced the Plecoglossidae to a subfamily of Osmeridae, Chapman (1941, 1941*a*) has presented numerous basic characters indicating they require familial status. A few such characters by which the Plecoglossidae may be separated from the Osmeridae are the 300 or

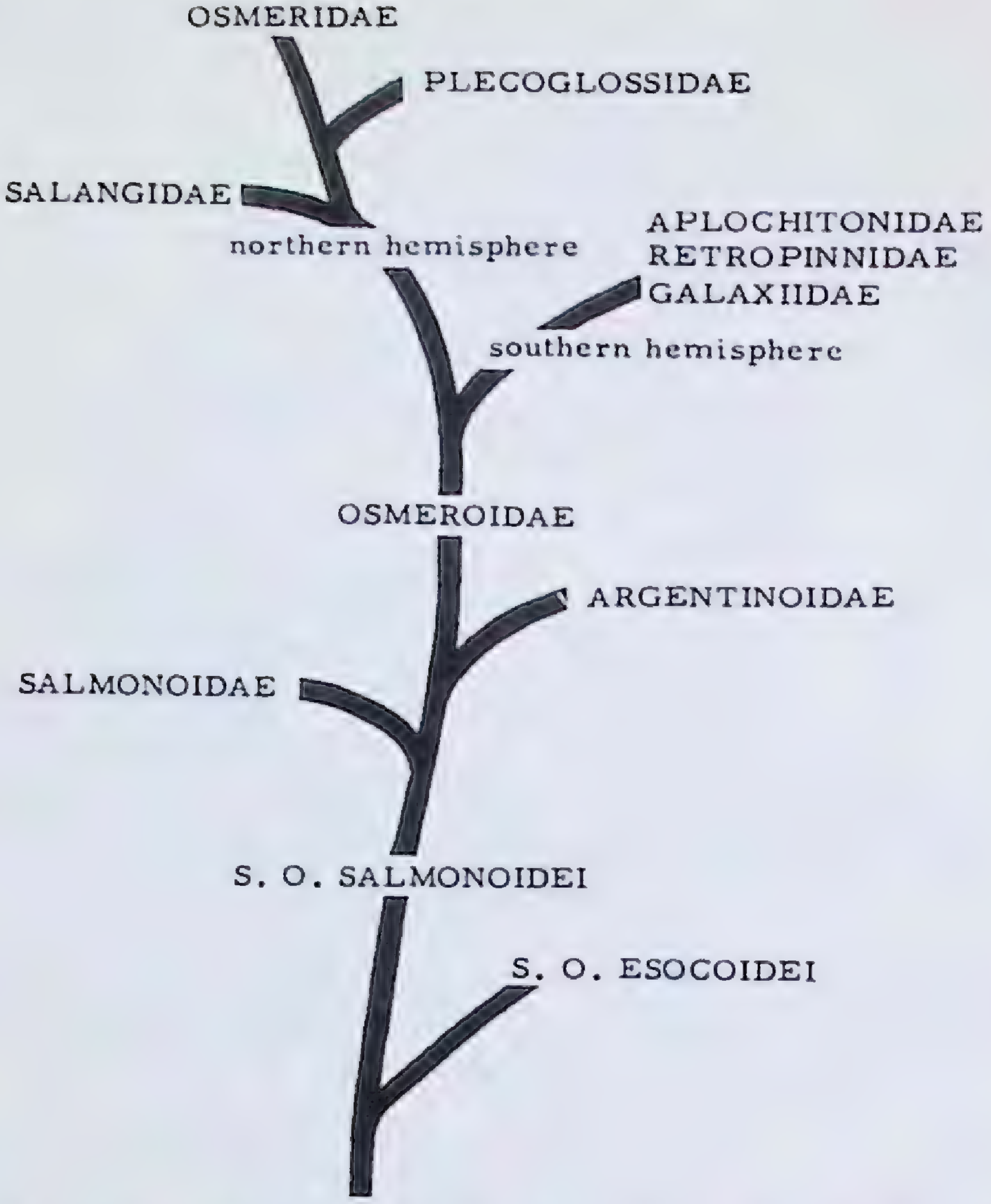


FIGURE 2. Relationships of the smelt family, Osmeridae (after Gosline, 1960).

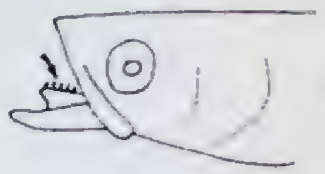
more pyloric caeca (as opposed to 0 to 11 in Osmeridae), the branchiostegals 6 or less (6 to 10 in Osmeridae), the uppermost branchiostegal expanded and crescentic, the peculiar comb-like sets of teeth, the absence of vomerine teeth, and the presence of a unique oral organ. The neotenic Salangidae of eastern Asia strongly resemble larval Osmeridae but may be distinguished by their reduced pointed head and elongated anterior portion of the body, as well as osteological characters. All these three northern hemisphere families are separated from the three southern hemisphere osmeroid families, Aplochitonidae, Retropinnidae, and Galaxiidae, by caudal osteology and other characters (Gosline, 1960), indicating separate evolution of each line after an initial crossing of the equator.

SUBFAMILIES

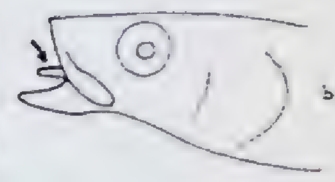
Berg (1940) recognized two subfamilies, Osmerini and Hypomesini [*sic*] (improper endings) although he was uncertain as to the allotment of the genera. Chapman (1941) after an osteological study did not recognize subfamilies. He did recognize the fundamental divergence between the two subfamilies here accepted but declined to establish subfamilies because of the intermediacy of *Spirinchus* in vomerine dentition and incomplete separation of the parietals by the supraoccipital. Although *Spirinchus* is intermediate in these two characters, there are at least twelve other sound characters, including osteological features, which separate the two groups. The author therefore recognizes two subfamilies, Osmerinae (*Spirinchus, Osmerus, Thaleichthys, Allosmerus*) and Hypomesinae (*Hypomesus, Mallotus*), based largely on osteological characters from Chapman.

ARTIFICIAL KEY TO THE GENERA

1 (6) Gill-rakers on upper half of arch 8–14. Lacking strong concentric striae on both operculum and suboperculum. Pyloric caeca 0–8.
2 (8) Tongue teeth not villiform, but medium conical to large canine (*see* fig. a). Maxillary ending after the posterior border of the pupil (mouth closed).
3 (7) Pyloric caeca 4–8. Orbit diameter less than $\frac{4}{5}$ of caudal peduncle depth.
4 (5) An arc of minute pointed teeth across vomer. Gill-rakers on lower half of arch 24–32 ....*Spirinchus* Jordan and Evermann, p. 7
5 (4) One or two large canines on either side of vomer. Gill-rakers on lower half of arch 15–24 ....*Osmerus* Linnaeus, p. 15
6 (1) Gill-rakers on upper half of arch 4–6. With strong concentric striae on both operculum and suboperculum. Pyloric caeca 8–11.......................................*Thaleichthys* Girard, p. 22
7 (3) Pyloric caeca 0–1. Orbit diameter exceeds $\frac{4}{5}$ of caudal peduncle depth ....*Allosmerus* Hubbs, p. 24
8 (2) Tongue teeth minute, villiform (*see* fig. b). Maxillary ending before posterior border of orbit.
9 (10) Lateral line incomplete. Scales large, 51–73 along midline. Adipose oval; base short, 1.2 times orbit or less. Peritoneum lightly sprinkled with dots ....*Hypomesus* Gill, p. 27
10 (9) Lateral line complete. Scales minute, 170–220 along midline. Adipose subrectangular; base long, 1.5 times orbit or more. Peritoneum so densely speckled as to be almost black ....*Mallotus* Cuvier, p. 37



a)



b)

Subfamily OSMERINAE

Synonymy

OSMERINI Berg 1940, p. 240 (type genus: *Osmerus* Linnaeus)

Glossohyal teeth conical or canine. Maxillary extends past middle of pupil. Proethmoids double. Otolith bulla markedly wider anteriorly. Posterior myodome opening narrow. Pterosphenoid (formerly alisphenoid) wing joining prootic wing. Mandible shallow. Palatine prominently dumbbell-shaped. Dorsal edge of metapterygoid almost straight. Metapterygoid without dorsal vane over hyomandibular head. Dorsal fork of post-temporal long and slender. Frontal with lateral wings over orbit.

Four genera: *Spirinchus, Osmerus, Thaleicthys, Allosmerus*

Genus **Spirinchus** Jordan and Evermann

Synonymy

Spirinchus Jordan and Evermann 1896, p. 522, as subgenus (type species: *Osmerus thaleichthys* Ayres by original designation); raised to genus by Hubbs, 1925, p. 53.

Series of small teeth in arc across vomer. Palatine teeth small. Rectilinear striae present or absent on subopercle, weak concentric striae present or absent on opercle and subopercle. Distance from snout to dorsal origin shorter or longer than from dorsal origin to caudal base. A midlateral ridge and anal shelf sometimes present in male. No elongate midlateral scales in male. Gill-rakers 32 to 47. Pyloric caeca 4 to 8. Stomach with blind sac poorly developed or absent. Lower jaw spatulate. Anal rays 14 to 19, pectoral 10 to 12. Midlateral scales 54 to 65. Lateral line incomplete. Adipose base from two-thirds of to equal to orbit diameter. Orbit diameter two-thirds or less of caudal peduncle depth.

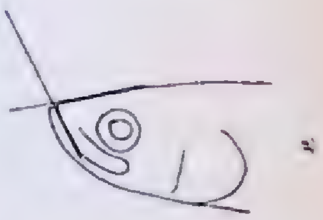
Proethmoids double. Mesethmoid with dorsal, ventral, and two lateral ossifications, all separated by cartilage. Parietals partially separated by supraoccipital, meeting anteriorly. Pterosphenoid not reaching parasphenoid wing anteriorly. No slit between hyomandibular and preopercular. Four simple actinosts (osteological characters from Chapman, 1941).

Three species: *Spirinchus lanceolatus, Spirinchus thaleichthys,* and *Spirinchus starksi,* marine and anadromous in the Pacific Ocean and its drainages.

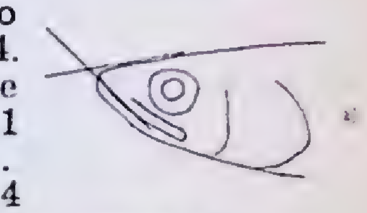
Key to the species of Spirinchus

1 (4) Weak horizontal striae on subopercle absent or less than three. Dorsal origin at or posterior to midpoint of body (to caudal base). Adipose fin length 1.7 times orbit or less. North American.

2 (3) Pectoral fin long, extending 84 per cent or more of the distance to the pelvic insertion. Midlateral scales usually 55–62. Vertebrae 55–61. Premaxillaries steep, forming an angle of 68°–90° to the forehead[1]; hence snout blunt (fig. a). Longest anal ray 1.4–2.2 times in head length. Males with anal shelf. Anadromous .... *Spirinchus thaleichthys* (Ayres), p. 10



3 (2) Pectoral fin short, extending 84 per cent or less of distance to pelvic insertion. Midlateral scales usually 62–66. Vertebrae 60–64. Premaxillaries more horizontal, forming an angle of 54°–65° to the forehead; hence snout pointed (fig. b). Longest anal ray 2.2–3.1 in head length. Males without an anal shelf. Marine .... *Spirinchus starksi* (Fisk), p. 14



4 (1) Several horizontal striae on subopercle (scrape off tubercles, if necessary). Dorsal origin anterior to midpoint of body (to caudal base). Adipose fin length 1.5 times or more diameter of orbit. Asiatic, Hokkaido. Anadromous.... .... *Spirinchus lanceolatus* (Hikita), p. 8

Spirinchus lanceolatus (Hikita) **shishamo** (Japanese)

Synonymy

Osmerus lanceolatus Hikita 1913, p. 127, pl., Muskawa River, Iburi Province, Hokkaido.

Diagnosis. Distinguished from other *Spirinchus* by the several longitudinal rectilinear striae on the suboperculum; the dorsal origin anterior to the midpoint of the body; the long adipose fin, 1.5 times or longer than the orbit.

Description. D 8–10; C 19; A 14–17; V 8; P 10–12; L.L. 13–19; midlateral scales 60–65; vertebrae 60–62; gill-rakers 11–13+24–28=36–40; branchiostegals 7–8; pyloric caeca 4–5.

Head length 4.2–4.4 in standard length; depth 4.7–5.7 in standard length; orbit 4.6–5.3 in head length. Maxillary terminating about under

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[1] For key purposes the angle may be measured by holding the head over a protractor.

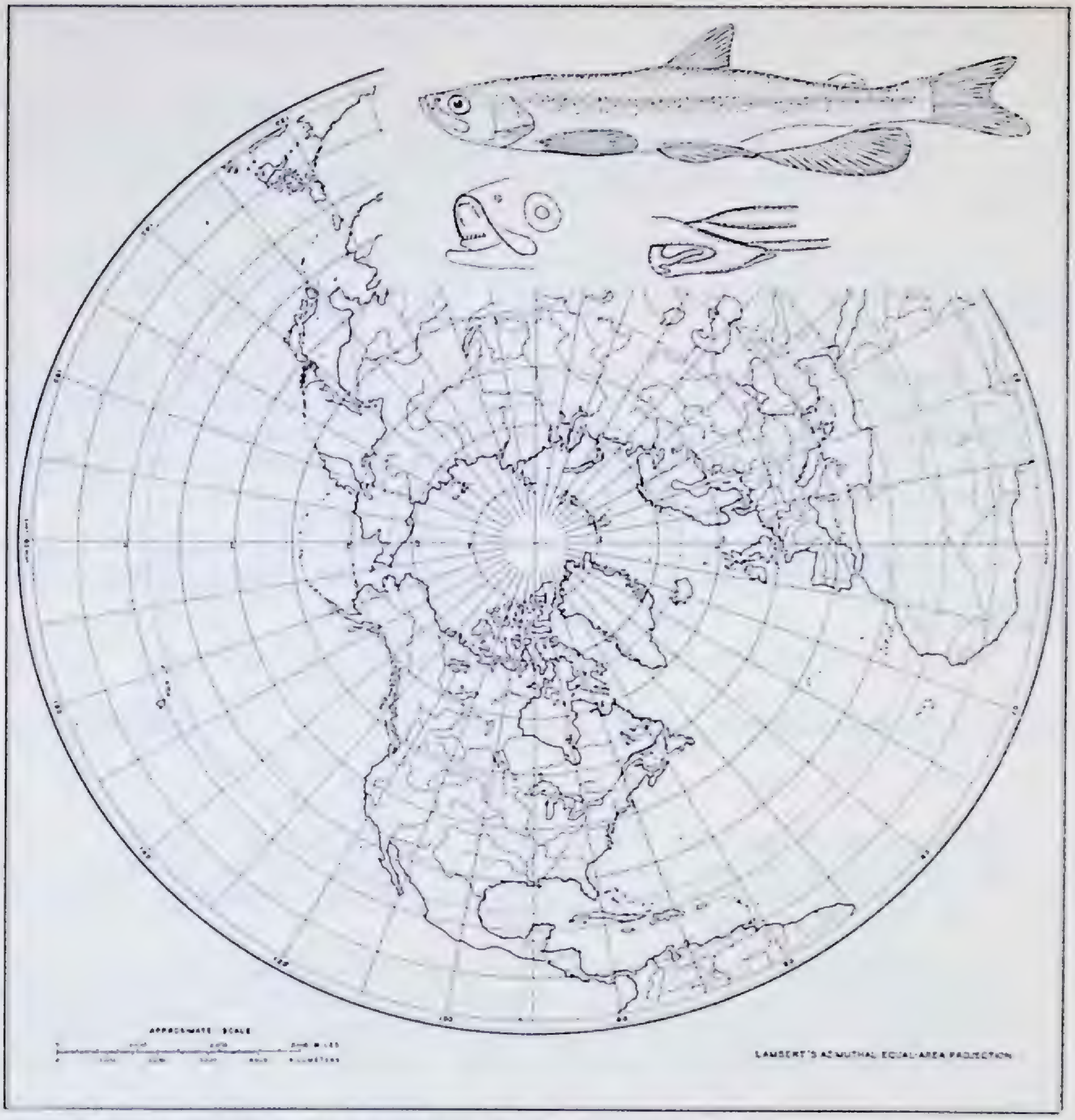


FIGURE 3. Distribution of *Spirinchus lanceolatus*. Inset shows lateral view of 140 mm male (BC56–349), dentition, intestines, and gas bladder.

posterior border of orbit. Pectoral not quite attaining pelvic, reaching 83–99 per cent of the distance to the pelvic insertion. Longest anal ray 1.6–2.5 in head length. Adipose fin large, 1.5 or more in orbit.

Pelvic insertion anterior to dorsal origin. Dorsal origin anterior to midpoint of body (to caudal base). Ductus pneumaticus attaches to anterior end of gas bladder. Lateral line incomplete, extending about a head's length along the body. Several horizontal striae on the subopercle (may be obscured by tubercles in the male). Gill-rakers long. Angle of premaxillaries to forehead 70 to 72 degrees.

Peritoneum silver with light speckling. Body brownish, darker dorsally, especially along the scale borders. Mature males darker, with dark mediolateral band.

Our longest specimen 141 mm standard length, the largest species of the genus.

Sexual dimorphism. Rays of paired and anal fins thickened and elongated; the paired fins tuberculated above and below in males. An anal shelf develops in males (*see* fig. 3 of male). The males become darker, head punctate.

Life-history. Anadromous. Spawns in rivers at night from June to August. Reaches maturity in 3 to 4 years. Hikita (1958) reports on its life-history and development.

Systematics. Spirinchus lanceolatus shares characters with both other species of the genus but appears most close to *S. thaleichthys,* particularly in the characters of the spawning male and in the anadromous habit. But, as shown in the key, *S. lanceolatus* is a distinct species from *S. thaleichthys.* Further, their spawning times are asynchronous.

Material examined. BC60–154: seven specimens from Shokotsu River, Hokkaido; BC56–348: two from "Japan"; BC56–349: four specimens from Hokkaido.

Range. Restricted to the eastern coast of Hokkaido, Japan.

Spirinchus thaleichthys (Ayres) 1860 **longfin smelt**

Synonymy

Osmerus thaleichthys Ayres 1860, p. 62, fig. 12, San Francisco.

Spirinchus dilatus Schultz and Chapman 1934, p. 67, pl. II, fig. 1 and 2, 3 to 5 miles above mouth Nooksack River, near Ferndale, Washington (holotype: U. Washington Dept. Fish. No. 2336).

Diagnosis. Distinguished from other *Spirinchus* by the long anal rays, 1.4 to 2.2 in head; the low number of midlateral scales 55 to 62; the longer pectoral almost reaching or passing pelvic, 84 per cent or more of distance to pelvic origin; longitudinal striae on the subopercle absent or less than three.

Description. D 8–9(10); C 19; A (15)16–18(19); V 8; P 10–12; L.L. 14–21; midlateral scales (54)55–61(62,63); vertebrae (55)56–61; gill-rakers (10)11–13+27–34=(38)39–47; branchiostegals 7–8; pyloric caeca 4–6.

Head 3.7–4.6 times in standard length; depth 5.1–6.6 in standard length; orbit 3.6–4.5 times in head, orbit about equal to snout; maxillary short of to opposite posterior margin of orbit. Pectoral fin tip just short of to past the pelvic insertion, reaching (83)84 to 128 per cent of the distance to the pelvic insertion. Longest anal ray 1.4 to 2.2 times in head; adipose fin length 1.7 times orbit or less.

Pelvic insertion anterior to dorsal origin. Dorsal origin at or posterior to midpoint of body (to caudal base). Ductus pneumaticus attaches to anterior end of gas bladder. Lateral line incomplete, extending about a head's length along the body. None to three horizontal rectilinear striae on the suboperculum; sometimes weak concentric striae on the operculum. Gill-rakers long. Angle of premaxillaries to forehead 68 to 90 degrees; the

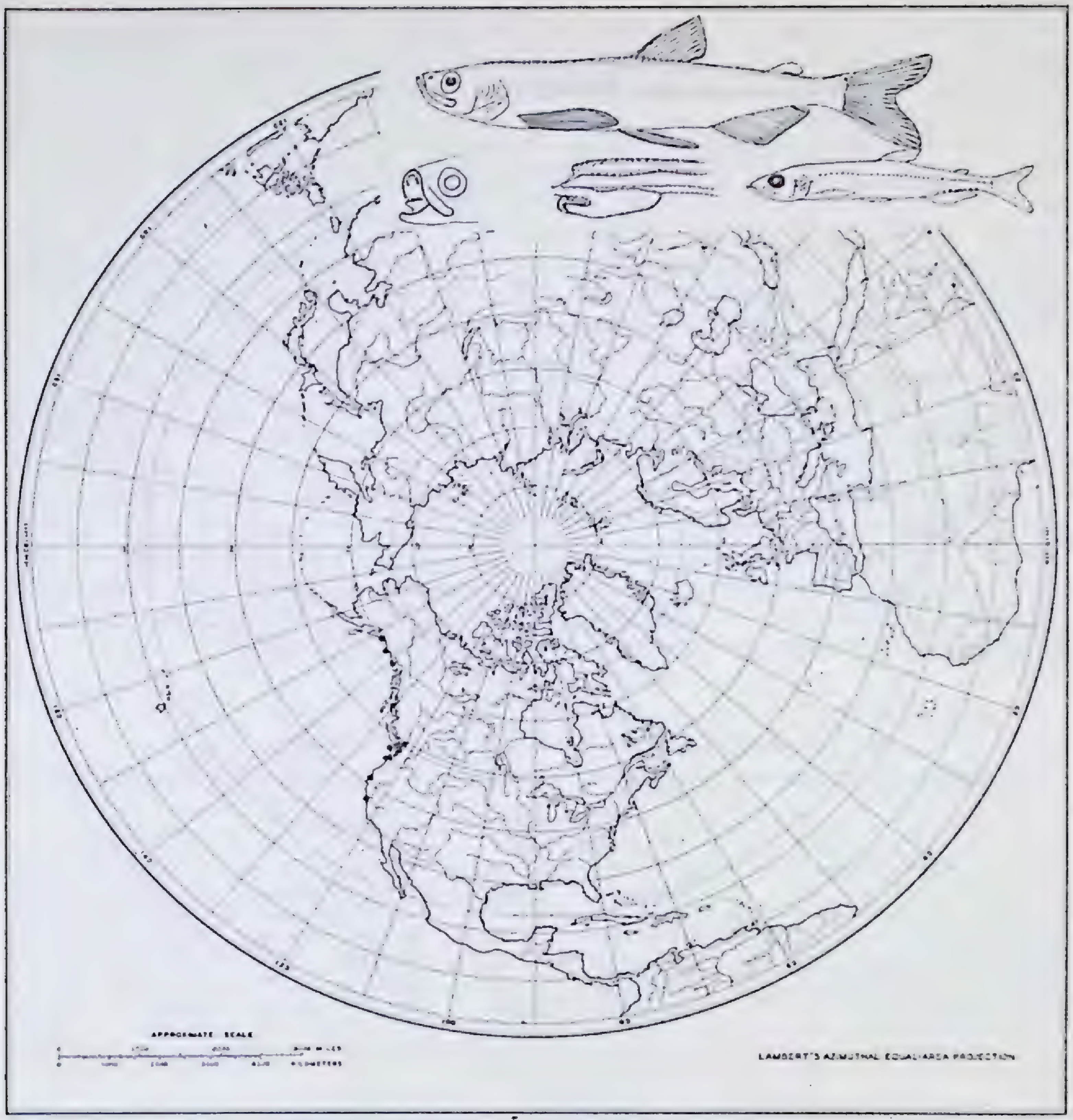


FIGURE 4. Distribution of *Spirinchus thaleichthys*. Inset shows lateral view of 109 mm specimen (OSC546), dentition, intestines, gas bladder, and 46 mm larvae.

premaxillaries tending toward the vertical making the snout obtuse (this character first noticed by Rosa, 1946).

Peritoneum silver with light speckling. Body brownish, darker dorsally, particularly along the scale borders. In life, back an olive-brown, sides silver.

Longest specimen examined 135 mm standard length (from British Columbia).

Sexual dimorphism. First ray of paired fins and rays of anal and dorsal fins enlarged and stiffened in males. Males lacking lateral silver band, and darker with profuse stippling on back and along scale margins.

The lateral line region is dilated by a swelling on the underlying muscles and the anal base is shelf-like in the males. Upper surface of paired fins and scales tuberculate in males (Schultz and Chapman, 1934; Rosa, 1946).

Life-history. Anadromous. Reported as apparently spawning in autumn in the north. Jensen (1957) took sexually mature fish in Eel River, California, on 1st December. Rutter (1908) noted adults ascending river to spawn in February, young descending in April. Food of young includes *Neomysis mercedis*, a shrimp-like form. Larger fish feed on euphausiids, copepods, and Cumacea. Few other details of life-history known (*See* Hart and McHugh (1944) and Rosa (1946)).

Systematics. In 1934 Schultz and Chapman named a new species of smelt, *Spirinchus dilatus*, from the Puget Sound area. They distinguished it from *S. thaleichthys* on the basis of shorter pectorals, more numerous scales and anal rays, and restricted the known distribution of *S. thaleichthys* to San Francisco Bay. With further material from Alaska (thanks to Robert Dryfoos, University of Washington), British Columbia, and Oregon, the attributed differences in the pectoral fin and mediolateral scales (and also vertebrae) are seen to be clinal in nature. The apparent differences between *S. dilatus* and *S. thaleichthys* were obtained by sampling different portions of this cline, as may be seen in the following table:

TABLE 1. Clines in *Spirinchus thaleichthys*

Province	Pectoral Length Pect.-Pelvic L.		Midlateral Scales		Vertebrae	
	Range	Mean	Range	Mean	Range	Mean
Alaska	.91–1.00	.96	57–62	60.4	58–61	60.0
British Columbia	.87–1.11	.94	57–63	60.5	57–61	59.7
Oregon	.94–1.15	1.02	56–60	58.4	57–59	58.0
California	1.02–1.28	1.14	55–61	58.2	55–58	56.6

The northward increase in number of vertebrae (with which scales are often correlated) is a well-known clinal phenomenon in fishes. Schultz and Chapman also noted a difference in the number of anal rays, with 17 to 20 in *dilatus* and 16 to 19 in *thaleichthys*. Because of the high degree of overlap in this character it cannot be accorded specific importance. No specific differences in other characters were discovered in this study. It is therefore necessary to consider *Spirinchus dilatus* a synonym of *S. thaleichthys*.

Lastly it may be noted that valid morphological and behavioural differences were found between *S. thaleichthys* (s. lat.) and *S. starksi*, as noted in the key. These two species are sympatric, having almost identical ranges. Both species were taken in one collection, *Albatross* Station 3099, San Francisco Bay.

Material examined. CAS21550: 12 specimens from San Francisco Bay; SU22612: one specimen from San Francisco Bay; OSC546: nine specimens from Columbia River at Astoria; B.C.55–359: two from San Juan Islands, Washington; BC60–324, BC59–530, BC56–647, BC57–32, BC57–302, BC56–649, BC57–304, BC53–77, BC53–127, BC53–58, BC53–55, BC53–49, BC53–303: 17 specimens from the Vancouver area, British Columbia; BC59–586: one from Dease Island Slough, British Columbia; BC57–29: three from Harrison Lake, British Columbia; UW15548: 12 from Prince William Sound, Hinchinbrook Island, Alaska.

Common name. With the synonymizing of the two species it is necessary to choose one of the two common names. Since *longfin smelt* is descriptively apt, and since *Sacramento smelt* is no longer an accurate geographical designation, the first is selected as the common name.

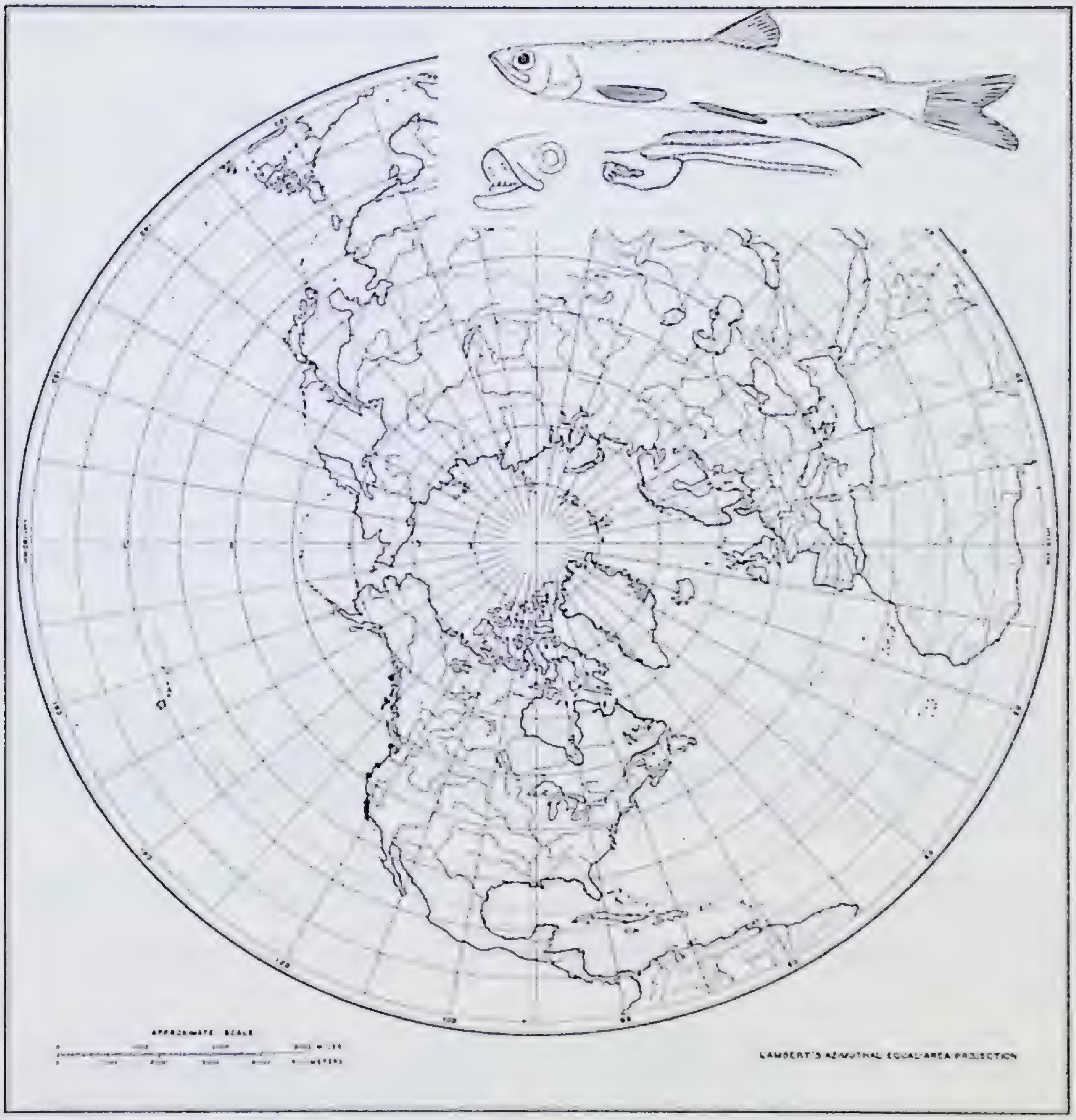


FIGURE 5. Distribution of *Spirinchus starksi*. Inset shows lateral view of 112 mm male (UW1856), dentition, intestine, and gas bladder.

Range. Occurs on the west coast of North America from Hinchinbrook Island, Prince William Sd., Alaska (Dryfoos, 1961) to San Francisco Bay, California.

Spirinchus starksi (Fisk) **night smelt**

Synonymy

Osmerus starksi Fisk 1913, p. 293, fig., market in San Francisco (holotype: U.S. Nat. Mus. 74834, paratypes Stanford University).

Diagnosis. Distinguished from other *Spirinchus* by the short anal rays 2.5–3.1 times in head; the more numerous midlateral scales, usually 62–65; the short pectorals reaching only 71 to 84 per cent of the distance to the pelvic insertion; and the presence of only three or less longitudinal rectilinear striae on the subopercle.

Description. D 8–9 (10); C 19; A 15–18 (19); V 8; P 10–11; L.L. 16–24; midlateral scales (60) 61–65 (66); vertebrae 60–63 (64); gill-rakers (8) 9–13+24–31=(32)33–44; branchiostegals 7–8; pyloric caeca (4)5–8.

Head (3.9) 4.0–4.7 times in standard length; depth 5.5–7.2 in standard length; orbit 4.0–4.8 in head length, orbit less than or equal to snout; tip of maxillary just short of to past posterior border of orbit. Pectoral fin not reaching pelvic insertion, extending (71) 72 to 84 (92) per cent of the distance to pelvic insertion. Longest anal ray 2.2 to 3.1 times in head length. Adipose fin length 1.7 times orbit or less.

Pelvic insertion anterior to dorsal origin. Dorsal origin at or posterior to midpoint of body (to caudal base). Ductus pneumaticus attaches to the anterior end of the gas bladder. Lateral line incomplete, extending less than a head's length along the body. None to three horizontal striae on the subopercle. Gill-rakers short. Angle of premaxillaries to forehead 54 to 65 degrees, the mouth being more horizontal and the snout more pointed (character first pointed out by Rosa, 1946).

Peritoneum silver with light speckling. Body brownish, darker dorsally particularly on posterior margins of scales. In life, back green, sides silver.

Longest specimen examined 112 mm standard length.

Sexual dimorphism. Pectoral fins tend to be longer in males. Lateral ridge and anal shelf absent or only slightly developed in males of this species. Tubercles on head, scales, and lower fins of males (Schultz and Chapman, 1934).

Life-history. Little known, probably spawns in surf at night. La Push, Washington, specimens were mature in May.

Systematics. Southern populations tend to have more gill-rakers and larger orbits.

Material examined. CAS25470: 12 specimens from San Simeon, California; SU47337: two specimens from off Pismo Beach, California; SU 41000: one specimen from Monterey Bay, California; SU22612: three specimens from *Albatross* Station 3099, San Francisco Bay, California; UW1856: 12 specimens from La Push, Washington; BC59-669: three specimens from

Hecate Strait between Cape Ball and Long (Lawn?) Point, the Queen Charlottes, British Columbia; UW15547: 12 specimens from Shelikof Bay, Alaska.

Range. Occurs on west coast of North America from Shelikof Bay, southeastern Alaska (Dryfoos, 1961) to Pt. Arguello, California.

Genus Osmerus Linnaeus

Synonymy

Osmeri Linnaeus 1758, p. 310, construed as *Osmerus* by Int. Comm. Zool. Nomencl. (type species: *Salmo eperlanus* Linnaeus by designation under the plenary powers of the Int. Comm., Direction 69; ex *Osmerus* Artedi).

Eperlanus Rutty 1772, p. 358 (type species: *E. Schonfoldii*=*Osmerus eperlanus* (Linnaeus), by monotypy).

One large canine on either side of vomer, sometimes accompanied by smaller ones. Palatine teeth enlarged anteriorly. Maxillary extends to about posterior border of orbit. No striae on opercle or subopercle. Distance from snout to dorsal origin shorter than from dorsal origin to caudal base. A midlateral ridge, but no anal shelf or elongated midlateral scales in male. Gill-rakers 25 to 37. Pyloric caeca 3 to 8. Stomach with blind sac. Lower jaw spatulate. Anal rays 11 to 16, pectoral 11 to 14. Midlateral scales 58 to 72. Lateral line incomplete. Adipose base about two-thirds of orbit diameter (rarely in large specimens equal to orbit). Orbit diameter two-thirds or less of caudal peduncle depth.

Proethmoids double. Mesethmoid simple, without other ossifications. Parietals completely separated by supraoccipital. Pterosphenoids not reaching parasphenoid anteriorly. Slit present between hyomandibular and preopercular. Four simple actinosts.

One species with two subspecies: *Osmerus eperlanus eperlanus* and *Osmerus eperlanus mordax*. Anadromous or landlocked in the Pacific, Arctic, and Atlantic oceans and their drainages.

Key to the Subspecies of Osmerus eperlanus

1 (2) Pored scales in the lateral line usually 14–28 (rarely 13–30). Western Atlantic, Pacific, and Arctic west to the White Sea and their drainages.. *Osmerus eperlanus mordax* (Mitchill), p. 15

2 (1) Pored scales in the lateral line usually 6–13 (rarely 0–16). Baltic and North seas and their drainages and upper Volga River.. *Osmerus eperlanus eperlanus* (Linnaeus), p. 20

Osmerus eperlanus mordax (Mitchill)

rainbow smelt
kyuri-uo (Japanese)
asiatskaya korioshka (Russian)

Synonymy

Atherina mordax Mitchill 1814, p. 15, New York (Speirs, 1951, indicated that this was the type description).

Osmerus viridescens Le Sueur 1818, p. 230, coast of Maine.

Osmerus sergeanti Norris 1868, p. 93, Schuylkill River, New Jersey (described but not named by Norris 1862, p. 58; *sergenti* auctorum).

Osmerus spectrum Cope 1870, p. 490, Wilton Pond, Kennebec County, Maine.
Osmerus abbottii Cope 1870, p. 490, Cobessicontic Lake, Kennebec County, Maine.
Osmerus dentex Steindachner, 1870, p. 429, Dekastris Bay, USSR.
Osmerus dvinensis Smitt 1882, p. 32, northern Dvina River, Russia (=*dwinensis* of authors).

[The following natios named by Petrov 1925, p. 82, 108, have no status under the rules of the Int. Comm. Zool. Nomencl.: *Osmerus e. dentex* natio *kaninensis,* Choshskaya Gulf; *O. e. dentex* natio *jenisseensis,* Enisi River at Tyurinu.]

Diagnosis. Distinguished from other osmerid species by the two large canines, one on either side of the vomer, the large midlateral scales 61 to 69; the absence of opercular striae; the maxillary extending past the pupil; 4 to 8 pyloric caeca. This subspecies is distinguished from *O. e. eperlanus* by the greater number of pored lateral line scales, usually 14 to 28.

Description. D 8–10(11); C 19; A (12)13–15(16); V 8; P 11–13(14); L.L. (13,14)15–28(29,30); midlateral scales (62)63–69(72); vertebrae (58,59)60–66(67,68,70); gill-rakers 8–11+18–24=(26)27–36(37); branchiostegals (6)7–8; pyloric caeca 4–8.

Head 3.8 to 4.4 in standard length; depth 4.7 to 7.4 in standard length. Pectorals reaching from one-half to two-thirds the distance to pelvic insertion; pelvics a little more than half to anal origin. Adipose base short, about two-thirds of eye diameter.

Medium-sized canines on dentary, enlarging posteriorly. Small pointed teeth on premaxillary and maxillary. Canines on anterior end of tongue enlarged. Pelvic origin anterior to dorsal origin. Ductus pneumaticus attached to anterior end of gas bladder. Lateral line incomplete, ceasing about a head's length along the body.

Peritoneum light with dark speckles, more intense dorsally. Ventral portion of body pale, dorsum speckled with black, more intensely around exposed borders of scales. Chin and top of head evenly speckled. A dark mediolateral bar without sharply delimited border. In life, sides an iridescent silver, the back an olive green.

Total length to 324 mm according to Berg (1948). The largest specimen examined was 257 mm in standard length (Herschel Island, Yukon, Canada). A larger subspecies than *O. e. eperlanus.*

Sexual dimorphism. Paired and anal fins slightly larger in males. Large tubercles on scales; small ones on head and leading rays of dorsal, anal, caudal, and paired fins of males. Tubercles reduced in females. There is a tendency in the males for a lateral muscular ridge to form, to be darker and to have a punctate operculum.

Life-history. An anadromous or landlocked species. Spawns in rivers not far above tidewater (anadromous races) in spring, February to June. Eggs hatch in about 8 to 27 days and drop down to the sea in the summer of the same year. Food consists of small crustacea, nereid worms, squid, and for adults, fishes to a large degree. Their enlarged canine teeth appear to be an adaption to their more piscivorous diet. They do not usually mature till their second year. Smelt appear to readily adapt to a completely freshwater existence, and natural freshwater populations are common in eastern North America. They have been introduced into the upper four Great Lakes where they have multiplied greatly and are the basis of a good-sized

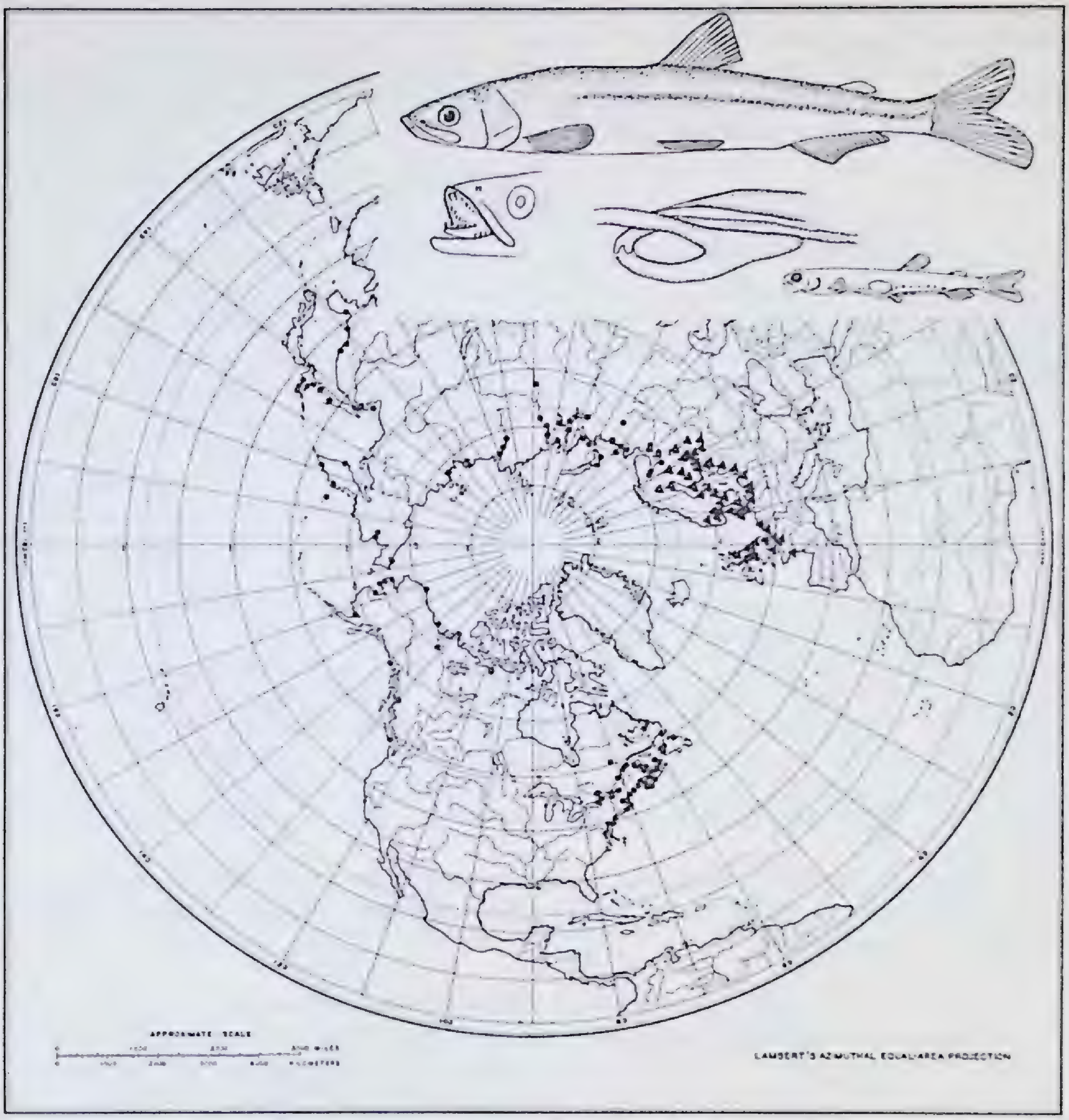


FIGURE 6. Distribution of *Osmerus eperlanus mordax*—circles, and *O. e. eperlanus*—triangles. Inset shows lateral view of 138 mm *O. e. mordax,* dentition, intestines, gas bladder, and 28 mm larval *O. e. eperlanus* after Ehrenbaum.

fishery (*see* Dymond, 1944). Further life-history notes may be obtained from Marcotte and Tremblay (1948), Kendall (1927), McKenzie (1958), Nordqvist (1910), and Langlois (1954).

Systematics. Three forms of the boreal smelt have generally been recognized: *O. eperlanus* of the North and Baltic seas; *D. dentex* of the Pacific north into the Arctic and west to the White Sea; and *O. mordax* of the western Atlantic. Following detailed studies of their populations, Berg, Andriashev, and other Russian workers have reduced *dentex* to a subspecies of *eperlanus.* Biologists bordering on the Pacific or Atlantic, having little occasion to compare them, have usually accorded specific distinction to *mordax* and *dentex*.

Hubbs (1925) separated the Atlantic American form into two types, a northern *O. mordax* (north of New York) and a southern *O. sergeanti* using the following characters:

	O. mordax	*O. sergeanti*
gill-rakers	10–11 + 19–24	9–10 + 15–18
height of anal in head	2.6–3.4	2.4–2.6

New Brunswick specimens of *mordax* were found to bear 8–11+10–22=28–33 gill-rakers and have a head/anal ratio of 2.4–2.9 and New York specimens with 10–11+18–22=28–32 gill-rakers and a head/anal ratio of 2.5–2.7, thus bridging the differences between the suggested northern and southern forms. Further, Fowler (1906) reports a New Jersey specimen with gill-rakers 10+19=29. No other differences have been found, and the modern tendency to consider *sergeanti* a synonym of *mordax* is followed.

The next problem to be examined is whether *mordax* (s. lat., including *sergeanti*) can be differentiated from *dentex*. Hubbs (1925) admitted that gill-rakers and the anal ratio failed to separate *mordax* (s. lat.) from *dentex*. In this the author concurs. The only reliable difference found by Hubbs was the backward extension of the jaw. But he admitted this character was not wholly constant. Comparison of 45 specimens of *dentex* (Japan and Alaska) and *mordax* (Quebec, New Brunswick) shows no significant difference in this character; in 15 *dentex* and 14 *mordax* the maxillary failed to reach the posterior border of the orbit, and in 8 *dentex* and 8 *mordax* the maxillary was opposite the posterior edge or past the orbit. Thus this character cannot be used to separate *dentex* and *mordax*.

Other characters of *dentex, mordax,* and *eperlanus* are compared in Table 2. Data are from Berg (1948), Kirpichnikov (1935), Jensen (1949), and the present study.

TABLE 2. Comparison of different forms of *Osmerus*

Character	*dentex*	*mordax*	*eperlanus*
L.L.	15-28 (13-30)	14–19 (13–19)	6–13 (0–16)
Vertebrae	63–66 (59–70)	60–63 (58–65)	58–61 (55–63)
Head l./anal height	2.6–3.2	2.3–4.4	2.3–2.6
Modal anal rays	13–14	13–15	12–13
Dorsal rays	8–10	9–10	7–9
Pectoral rays	12–13	(11)12–13	11–12(13)
Midlateral scales	63–72	63–65	61–69
Gill-rakers	26–35	28–35	25–37
Pyloric caeca	5–8	4–7	3–7

The above table shows no differences worthy of subspecific differentiation between *dentex* and *mordax*, except perhaps that of vertebrae. Using vertebral counts from Kirpichnikov (1935) from the White Sea area and from Marcotte and Tremblay (1948) from Chaleur Bay – St. Lawrence estuary area, one is able to separate 94 per cent of all the specimens of both species (61 *dentex* and 2,887 *mordax* have 63 vertebrae or less, and 647 *dentex* and 66 *mordax* have 64 or more vertebrae). Of 31 Alaskan specimens examined, only 90 per cent could be separated from *mordax* (in Chaleur Bay–St. Lawrence sample). This is slightly below the 93 per cent separation for subspecies recommended by Bailey, Winn, and Smith (1954). The single southernmost specimen of *dentex* available from British Columbia had 63 vertebrae, intimating even poorer separation.

However, doubt must be cast upon even this level of separation attained. First, the samples represent only a small part of the range of these forms, only the northwestern limits of *dentex* and only a segment of the central portion of the range of *mordax*. Much greater variability must thus be expected when fuller investigations are made. Secondly, it may be noted that *mordax*, which inhabits more southerly latitudes, has fewer vertebrae than *dentex*. This is typical of clinal variation in fishes and was also found in *Spirinchus thaleichthys*. If the vertebral differences are only the result of northward increase of vertebrae in a cline, then the differences cannot be used to indicate phylogenetic differences. No other differences having been found, it is therefore necessary to consider *dentex* a synonym of *mordax* (*mordax* having priority).

It is now necessary to compare *mordax* (s. lat, including *dentex*) with *eperlanus*. Referring to the above table, it will be seen that there are no non-overlapping characters and that only the number of pored lateral line scales separates the two with any degree of completeness. The data for this character are now analysed more carefully.

	Locale	*Number of pored lateral line scales*	
		4–13	14–28
mordax	White Sea	1	260
	Alaska – British Columbia	0	12
	Yukon	0	4
	Japan	0	2
	Newfoundland	0	16
	Ontario	2	8
	Michigan	0	10
	Quebec	0	2
	New York	0	10
eperlanus	Baltic	343	0

Data are from Kirpichnikov (1935) and the present study. Using this character alone, over 99 per cent of all the specimens of both forms can be separated. Poll (1947) and Day (1880) indicate Belgian and English specimens agree with Baltic *eperlanus* in low counts, 7 to 11. Since the two forms are allopatric and since vertebral and anal ray differences all overlap considerably, it is necessary to consider the two forms as subspecifically different. The difference is non-clinal since populations of *mordax* south of *eperlanus* still have more pored scales. One is able to conclude, therefore, that there are two subspecies of boreal smelt: *Osmerus eperlanus eperlanus* of the Baltic and North seas, and *Osmerus eperlanus mordax* of the western Atlantic, Pacific, and Arctic oceans.

Should sympatric populations of the two forms be found, which did not interbreed, it would then be necessary to consider them full species.

Zoogeography. A short comment is necessary to explain the unusual distribution of the two subspecies, particularly the Arctic hiatus of *O. eperlanus mordax* (*see* distribution map).

The simplest explanation of this distribution involves an origin of the species in the North Pacific or adjacent Arctic. Spread then took place, westward along Arctic Russia to the White Sea. From the White Sea they were either "sluiced-up" in proglacial lakes or dammed in front of advancing Pleistocene glaciers and carried into the Baltic. Or they may have migrated around Scandinavia to the Baltic while isotherms were depressed southward during glaciation (from Segerstrâle, 1957). In either case, following deglaciation, the populations were left stranded in lakes and cooler portions of the Baltic to slowly undergo adaption to higher temperatures and lowered salinities, the intervening populations along the outer Norwegian coast disappearing. During the resultant isolation the present *eperlanus* type evolved.

The origin of eastern North American *mordax* from western North America populations of the subspecies can be ascribed to a migration across Arctic Canada during a more recent interglacial period or during the warm postglacial hypsithermal period. Cooling then resulted in the present separation of populations. If the migration took place during an interglacial period, one may assume that intermixing took place during the hypsithermal, thus preventing differentiation of east and west populations. Thus the two subspecies, one with disjunct distribution, can be readily derived.

Material examined. NMC59–332A, NMC59–326, NMC59–329: 20 from Passamaquoddy Bay, New Brunswick; BC59–287: two from Bay of Fundy, New Brunswick; NMC60–34: two from Matane, Quebec; BC59–285: one from Barkley Sound, British Columbia; BC58–306 and BC60–459: nine from Bristol Bay, Alaska; Wilimovsky collection Sta. 43–6 (now at U.B.C.): seven from Chukchi Sea at 66° 43.5′ N., 166° 14′ W.; BC60–377: one from Bering Sea between Nome and Safety Sound; BC60–154: four from Shokotsu River, Hokkaido.

Common name. With the uniting of *dentex* and *mordax,* the common names "American smelt" and "Arctic smelt" become inapplicable. The common name *rainbow smelt* is therefore suggested, in allusion to its iridescent hues when alive.

Range. South to Barkley Sound, Vancouver Island, British Columbia, in the east Pacific; south to Wonsan, Korea, in the west Pacific; in the Arctic east to Cape Bathurst, Northwest Territories, west to the White Sea. The northernmost point is on the southern island of Novaya Zemlya. In the western Atlantic it is known from Pike Run Cove, Lake Melville, Labrador south to Delaware River, Pennsylvania, and questionably to Virginia.

Osmerus eperlanus eperlanus (Linnaeus)

rainbow smelt
l'éperlan (French)
stint (German)
smaelt (Dutch)
korioshka (Russian)
nors (Norway, Sweden)

Synonymy

Salmo eperlanus Linnaeus 1758, p. 310, European seas and rivers (ex Artedi; *Osmerus eperlanus* placed on Official List of Specific Names in Zoology by Int. Comm. Zool. Nomencl., Direction 69).

Eperlanus Schonfoldii Rutty 1772, p. 358, Ireland (*fide* Day 1884).

Salmo eperlano-marinus Bloch 1782, p. 229, tab. 28, fig. 1, northern and Baltic seas and into rivers.

Salmo eperlanus var. *marinus* Walbaum 1792, p. 57.

Salmo spirinchus Pallas 1814, p. 387, lakes and rivers Germany, European Russia, Beloozero, Chudsk. (*ex parte*).

[*Eperlanus Rondeletii* Willughby 1789, p. 202, tab. 6, fig. 4, anadromous in Thamesi (unavailable since it is a reprint of a pre-Linnaean 1686 edition).]

Salmo eperlanus marinus Walbaum 1792, p. 57 (ex Bloch).

[*Eperlanus fluviatilis* Gesner in the synonymy for *Salmo eperlanus* of Donovan 1804, p. 189 (not available, a pre-Linnaean name cited in a synonymy).]

Eperlanus vulgaris Gaimard 1851, p. 207, p. 18, fig. 2, Island (=Iceland; this species not known in Iceland before or since this time according to Saemundsson, 1949).

[*Osmerus e. eperlanus* natio *ladogensis* Berg 1932, p. 281, Lake Ladoga (infrasubspecific names have no status under the Int. Rules Zool. Nomencl.).]

Diagnosis. Distinguished from other osmerid species by the two large fangs, one on either side of the vomer, the large midlateral scales 61 to 69, the absence of opercular striae; the maxillary extending past the pupil; pyloric caeca 4 to 8. This subspecies is distinguished from *O. e. mordax* by the lower number of pored lateral line scales, 4 to 13.

Description. D 7–9; C 19; A (11)12–13(14); V 8; P 11–12(13); L.L. (0)4–13(16); midlateral scales (58)61–69; vertebrae (55,56)57–61(62,63); gill-rakers 25–37; branchiostegals 7(8); pyloric caeca 3–7.

Head length about 4 to 5 times in standard length; depth 5.6 to 6.1 in standard length; pectorals extend one-half to two-thirds the distance to the pelvic insertion; pelvics about halfway to anal origin. Adipose base short, about two-thirds the orbit diameter.

Medium-sized canines on dentary, enlarging posteriorly. Small pointed teeth on premaxillary and maxillary. Ductus pneumaticus attached to anterior end of air bladder. Lateral line incomplete ceasing less than a head's length along the body.

Peritoneum light with dark speckles. Back greenish, sides silver in life. (For distribution *see* Figure 6.)

Total length to 307 mm according to Berg (1948). A smaller form than *O. e. mordax.*

Life-history. Anadromous or landlocked. Spawns in rivers from March to July. Feeds on fish, particularly herring, crustacea, and worms.

Systematics (*See* under *O. e. mordax*).

Material examined. Description in part from Berg (1948), Smitt (1895), and Kirpichnikov (1935).

Range. The Baltic and North seas and their drainages southward, including England to the mouth of the Loire River, France. Icelandic, Irish, and Spanish records have not been authenticated. Although Zenkevich (1957) mentions Osmeridae in the Caspian Sea, it is here omitted since Berg (1948) does not record it. It is, however, known from the upper Volga.

Genus Thaleichthys Girard

Synonymy

Thaleichthys Girard 1858, p. 325 (type species: *Thaleichthys stevensi* Girard = *Thaleichthys pacificus* (Richardson), by monotypy).

Eperlanio Jordan 1918, p. 34 (type species: *Osmerus albatrossis* Jordan and Gilbert = *Thaleichthys pacificus* (Richardson), by monotypy).

Vomer with two moderate canines. Palatine teeth larger anteriorly. Concentric striae on opercle and subopercle. Distance from snout to dorsal

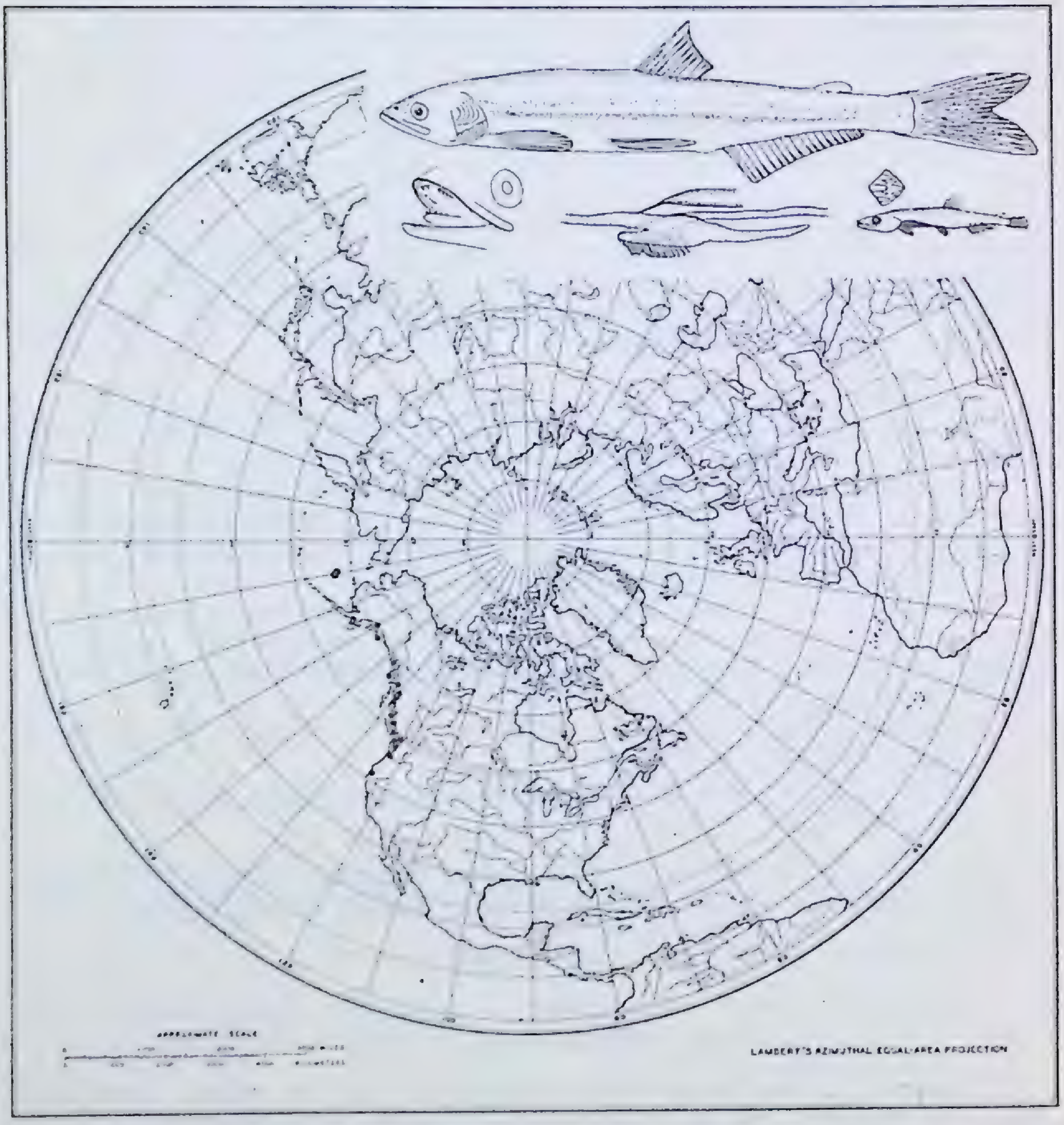


FIGURE 7. Distribution of *Thaleichthys pacificus*. Inset shows lateral view of 162 mm male (BC59–303), dentition, intestine, gas bladder, male tubercular scale, and 57 mm larva after Chapman (1939).

origin usually longer than from dorsal origin to caudal base. Midlateral ridge but no anal shelf or elongate midlateral scales in male. Gill-rakers 17 to 23. Pyloric caeca 8 to 11. Stomach with blind sac. Lower jaw spatulate. Anal rays 18 to 23, pectoral 10 to 12. Lateral line complete with 70 to 78 scales. Adipose base about two-thirds the orbit. Orbit diameter less than two-thirds depth of caudal peduncle.

Proethmoids double. Mesethmoid with dorsal, posterior, ventral, and two lateral ossifications, all separated by cartilage. Parietals completely separated by the supraoccipital. Pterosphenoids, reaching parasphenoid anteriorly. A slit between hyomandibular and preopercular. Four simple actinosts (osteological characters from Chapman, 1941).

One species: *Thaleichthys pacificus.* Anadromous on the west coast of North America.

Thaleichthys pacificus (Richardson) **eulachon**

Synonymy

Salmo (Mallotus) pacificus Richardson 1836, p. 226, Columbia River.
Thaleichthys stevensi Girard 1858, p. 325, pl. 76, fig. 1–4, Puget Sound, Washington (Plate labelled *Osmerus stevensi,* in error).
Osmerus albatrossis Jordan and Gilbert 1898, in Jordan and Evermann 1898, p. 2823, *Albatross* Station 3675, Shelikof Straits, north of Karluk, Alaska.
Lestidium (Bathysudis) parri Chapman 1939, p. 522, fig. 64, off Prince William Sound, Alaska (holotype: U. S. Nat. Mus. 108140).

Diagnosis. Distinguished from other osmerids by the strong concentric striae on the operculum and suboperculum and the low number of gill-rakers on the upper half of the arch, 4 to 6.

Description. D 10–12(13): C 19; A 18–22(23): V 8; P 10–12; L.L. 70–78; vertebrae 65–72; gill-rakers 4–6+13–18=17–23; branchiostegals (6)7–8; pyloric caeca 8–11.

Head 3.8 to 5.0 times in standard length; depth 5.0 to 6.8 times in standard length. Pectoral extending two-thirds the distance to pelvic insertion. Anal base long, almost equal to head length. Pelvic origin anterior to dorsal origin. Gill-rakers slender, length about two-thirds of orbit diameter. Base of adipose fin less than orbit diameter.

Teeth tend to be lost in spawners, particularly males. Others with small pointed teeth on dentary, maxillary, premaxillary. Lateral line complete.

Peritoneum light with black speckles. A bluish brown on upper parts with silver white on sides and venter. Black stippling on back sparse, fine.

Maximum length reported to 300 mm. Hart and McHugh (1944) reported the largest examined from British Columbia not to be much over 200 mm. Taranetz (1933) gives the fork length in Bering Strait specimens as up to 225 mm.

Sexual dimorphism. Males with midlateral ridge formed by the thickening of the lateral muscles. Males with numerous tubercles on head, body, upper side of paired fin and anal rays. Those on the scales of the upper side of the body are oval shaped (*see* inset in figure). In females tuberculation much reduced. Base of anal fin larger in males and pelvics often reaching to anus or anal fin. The pelvics fall far short of the anus in the females.

Life-history. An anadromous species. Spawns from March to middle of May in British Columbia rivers on pea-sized gravel or sand. The outer membrane of the egg breaks off, except at one point, and becomes attached to sand particles. The hatched larvae are carried to sea by river currents soon after hatching. Adult food consists mainly of euphausids and cumaceans. (For further details *see* Hart and McHugh (1944) and Smith and Saalfeld (1955).)

The eulachon was of great use to native Indians for food and oil. It was traded long distances into the interior. Dried and supplied with a wick, it was formerly used for lighting purposes, hence its old name candlefish. The name "eulachon" is of native Indian derivation. It is pronounced oolak-on.

Material examined. BC60–650: five specimens from English Bay, Vancouver, British Columbia; BC59–303: ten from Albion, Fraser River, British Columbia; BC55–52: one from Massis Point, British Columbia; BC53–302: two from off northeast coast of Denman Island, British Columbia; BC59–553: thirteen from Bear River at Stewart, British Columbia; BC58–200: one from Tidewater Slough, Cook Inlet, Alaska; BC59–285: one from Barkley Sound, Vancouver Island, British Columbia.

Range. Known in the eastern Pacific and its drainages from Klamath River, California, north to Nushagak River, Alaska, and the Pribilof Islands.

Genus Allosmerus Hubbs

Synonymy

Allosmerus Hubbs 1925, p. 53 (type species *Osmerus attenuatus* Lockington = *Osmerus elongatus* Ayres, by original designation).

Vomer with one large median tooth, sometimes flanked by one or two smaller. A large terminal glossohyal tooth. Teeth along palatine enlarged anteriorly. Sometimes concentric striae on subopercle. Snout to dorsal origin longer than from dorsal origin to caudal base. Anteriorly a midlateral ridge of elongate scales and a slight anal shelf in males. Gill-rakers 33 to 41. Pyloric caeca absent or a minute one. Stomach with blind sac. Lower jaw spatulate. Anal rays 14 to 17, pectoral 12 to 14. Lateral line incomplete. Midlateral scales 62 to 68. Adipose base about two-thirds the orbit. Orbit large, diameter four-fifths or more of caudal peduncle depth.

Proethmoids double, not fused. Mesethmoid ossified with posterior, ventral, and lateral ossifications. Parietals completely separated by supraoccipital. Pterosphenoids not reaching parasphenoid anteriorly. A slit between the hyomandibular and preopercular. Four simple actinosts (osteological characters from Chapman, 1941).

One species: *Allosmerus elongatus*. A marine form confined to western United States.

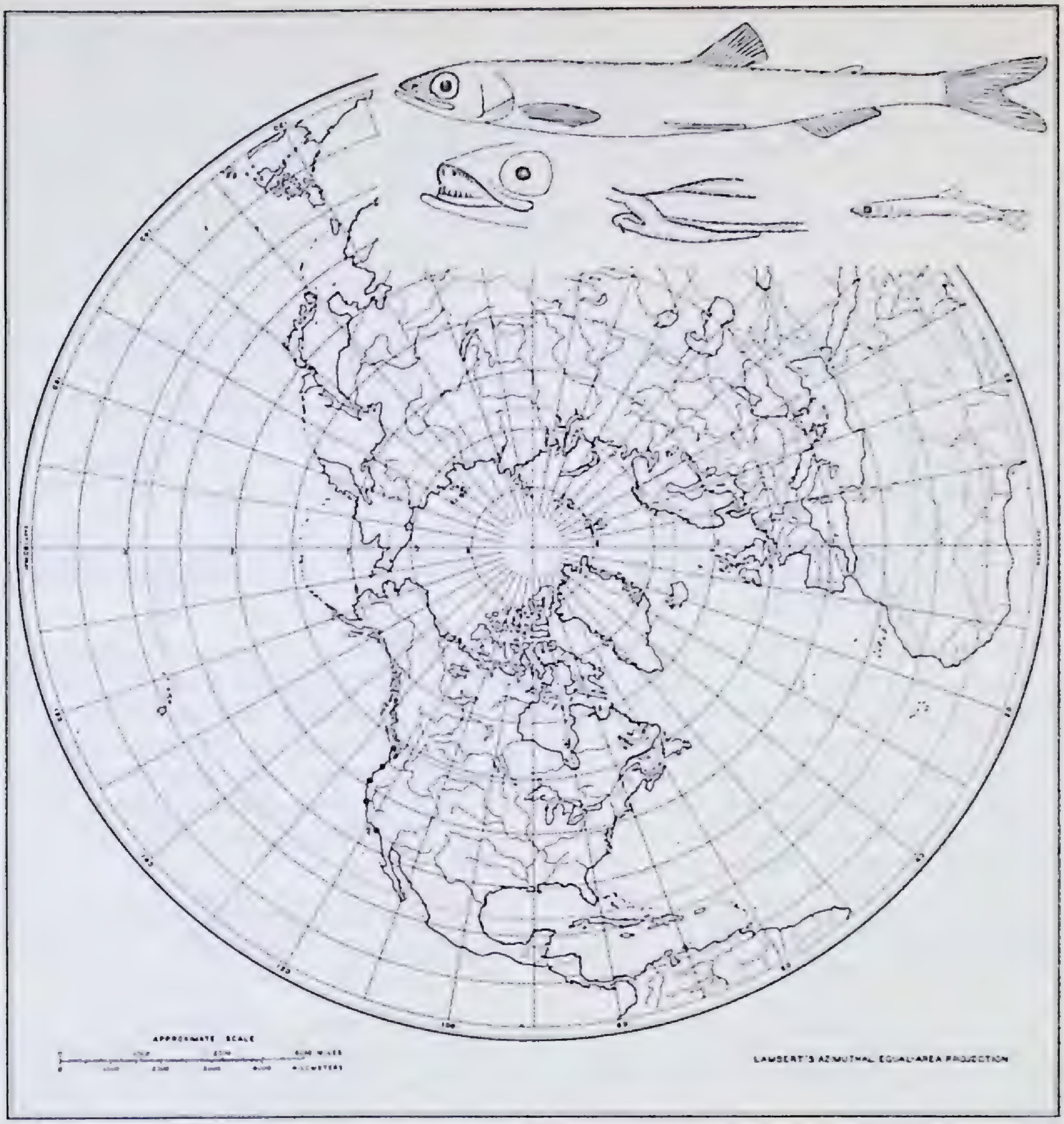


Figure 8. Distribution of *Allosmerus elongatus*. Inset shows lateral view of 109 mm specimen (CAS21581), dentition, intestine, and gas bladder, 62 mm larvae (The southernmost record is questioned as it may have been released live bait).

Allosmerus elongatus (Ayres) whitebait smelt

Synonymy

Osmerus elongatus Ayres 1854, p. 17, San Francisco, California.
Osmerus attenuatus Lockington 1880, p. 66, San Francisco, California.

Diagnosis. Distinguished by the single large canine on the middle of the vomer (occasionally a smaller canine on either side); the long, pointed snout and large eye, both of which exceed four-fifths of the caudal peduncle depth. The pyloric caeca, 0 to 1, separate it from all other Osmeridae except *Hypomesus olidus* (which is not known in the range of *Allosmerus*).

Description. D 9–10; C 19; A 14–17; V 8; P 12–14; L.L. about 20, midlateral scales 62–68; vertebrae 65–67; gill-rakers 10–13+23–28=33–41; branchiostegals 6–7; pyloric caeca 0–1.

Head 3.5 to 4.2 times in standard length; depth 6.5 to 9 times in standard length. Orbit large, 3.6 to 4.2 in head length; it and snout four-fifths or more of caudal peduncle depth. Pectoral reaching about halfway to pelvic, its length 53 to 64 per cent of the distance to the pelvic insertion. Length of adipose base about one-third of orbit. Pelvic origin in front of dorsal origin. Dorsal origin distinctly behind centre of body (to caudal base). Ventrals short of anal fin.

Medium teeth on dentary, premaxillary, maxillary. Gill-rakers short, length about one half of orbit. Scales deciduous.

Peritoneum light, speckled especially dorsally and anteriorly. In life, back greenish grey, sides with sharply-demarcated dorsal-edged silver stripe.

Maximum length to 229 mm, according to Roedel (1953).

Sexual dimorphism. Male with elongate midlateral scales anteriorly, with coarse tubercles on head, scales, median fin rays, and upper surface of rays of paired fins.

Life-history. Probably spawns in ocean. Development protracted, the young remaining in the translucent larval condition until a length of about three inches is reached (Hubbs, 1925). Little published life-history information. A mature male taken 28 March, 1961, Humbolt Bay, California.

Taxonomy. Rosa (1946) was the first to mention that *Osmerus attenuatus* and *O. elongatus* were conspecific. The original description of *elongatus* is poor but can be recognized since Ayres mentions the far-back position of the dorsal.

Material examined. CAS21581: seven from San Francisco Bay, California; CAS21365: two from San Francisco Bay; CAS21462: two from San Francisco Bay; NMC61–221: one from Eureka, California.

Range. Known on the west coast of United States from the Strait of Juan de Fuca, Washington, south to San Francisco Bay and possibly to San Pedro, California. (The latter may have been released live bait—Clark (1940).)

Subfamily HYPOMESINAE

Synonymy

HYPOMESINI Berg (1940), p. 240 (type genus: *Hypomesus*)
MALLOTINAE Fowler (1958), p. 7 (type genus: *Mallotus*)

Glossohyal teeth minute, velvet-like. Maxillary terminating at or before middle of pupil. Proethmoids fused. Otolith bulla not much wider anteriorly than posteriorly. Posterior opening of myodome broad. Pterosphenoid without posterior wing joining prootic wing. Mandible deep. Palatine hardly dumbell-shaped, appearing slender. Dorsal edge of metapterygoid with deeply rounded notch. Metapterygoid with broad dorsal vane extending up over articular head of hyomandibular. Dorsal fork of post-temporal short and broad. Frontal without lateral wing over orbit.

Two genera: *Hypomesus* and *Mallotus.*

NOTE: While this paper was in press, Wales (1962, Calif. Fish Game, p. 141) announced Japanese "*Hypomesus olidus*" were recently planted in California lakes and reservoirs. It is most likely that these were actually *H. transpacificus nipponensis,* but this has not been verified.

Genus Hypomesus Gill

Synonymy

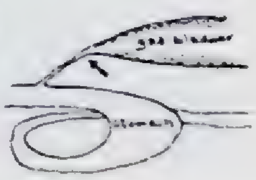
Hypomesus Gill 1863, p. 15 (type species: *Argentina pretiosa* Girard[1] by original designation: *Mesopus,* for the same entity, was left in type through failure to correct the proof sheets, on p. 14; Gill (1863*a*) later selected *Hypomesus* as the generic name).

Vomer with an arch of small teeth across it. Palatine teeth small. Maxillary terminates anterior to the middle of the pupil. No striae on opercular or subopercular. Snout to dorsal origin shorter than from dorsal origin to caudal base. No midlateral ridge, anal shelf or elongate midlateral scales in male. Gill-rakers 26 to 36. Pyloric caeca 0 to 7. Stomach not ending in blind sac. Lower jaw scoop-shaped. Anal rays 11 to 17, pectorals 10 to 17. Midlateral scales 51 to 73. Lateral line incomplete. Adipose base about two-thirds to a little more than orbit diameter.

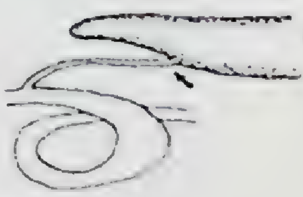
Proethmoids fused anteriorly, divergent posteriorly. Mesethmoid region covered by thin dorsal plate, no posterior, ventral, or lateral ossifications. Parietal not at all separated by supraoccipital. Pterosphenoids not reaching parasphenoid anteriorly. No slit between hyomandibular and preopercular. Four simple actinosts (osteological characters from Chapman, 1941). Hamanda (1957) was the first author to recognize the existence of three species of *Hypomesus.* He also has established their biological differences. However, his new specific name *sakhalinus* is a synonym of *olidus;* his *olidus* is an undescribed species *transpacificus nipponensis,* and his *japonicus* is *pretiosus japonicus.*

Three species, two with two subspecies each: *Hypomesus pretiosus pretiosus, H. pretiosus japonicus, H. olidus, H. transpacificus transpacificus, H. transpacificus nipponensis,* marine, anadromous, and freshwater in the Pacific and Arctic oceans and their drainages.

Natural Key to the Species and Subspecies of Hypomesus



a)



b)

1 (8) Pyloric caeca 4–7. Adipose base less than orbit diameter. Pneumatic duct attaches to anterior end of gas bladder (*see* fig. a). Marine and anadromous.

2 (5) Midlateral scales of 61 or more. Vertebrae 59–70. Longest anal ray 2.6–3.5 in head length. Eye (4.0)4.1–5.9 in head length. Marine .... *Hypomesus pretiosus* (Girard)

3 (4) Midlateral scales 66–73. Pectoral rays 14–17. Pectoral extending 41–48 per cent of distance to pelvic insertion. Dorsal origin posterior to midpoint of body (to caudal base). Vertebrae usually 64–67. North American coast .... *Hypomesus pretiosus pretiosus* (Girard), p. 28

4 (3) Midlateral scales usually 64–67. Pectoral rays usually 13–14. Pectoral extending 48–59 per cent of the distance to pelvic insertion. Dorsal origin anterior

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[1] Gill gave type as *Argentina pretiosa* of Girard or *Osmerus elongatus* of Ayres, incorrectly believing the latter to be a synonym of the former.

to midpoint of body (to caudal base). Vertebrae usually 62–65. Asiatic coast ....*Hypomesus pretiosus japonicus* (Brevoort), p. 30

5 (2) Midlateral scales 60 or less. Vertebrae 52–68. Longest anal ray 2.0–2.3 in head length; orbit 3.4–4.0 in head length. Euryhaline..*Hypomesus transpacificus* n. sp.

6 (7) Pectoral rays 10–12. Anal rays 15–17. Dorsal rays 9–10. One or no chromatophores between mandibles. Euryhaline. California...*Hypomesus transpacificus transpacificus*, p. 34

7 (6) Pectoral rays 12–14. Anal rays 13–15. Dorsal rays 7–9. Ten or more chromatophores between mandibles. Anadromous. Hokkaido..*Hypomesus transpacificus nipponensis* n. subsp., p. 36

8 (1) Pyloric caeca 0–3. Adipose base equals or exceeds orbit. Pneumatic duct attaches behind anterior end of gas bladder (*see* fig. b). Freshwater. Arctic and Pacific drainages........................*Hypomesus olidus* (Pallas), p. 31

Hypomesus pretiosus pretiosus (Girard) surf smelt

Synonymy

Argentina pretiosa Girard 1855, p. 150, Presido (San Francisco), California (Index Proc. Acad. Nat. Sci. gives indication publication date: received by Boston Soc. Nat. Hist. on 22 May 1855).

Diagnosis. Distinguished from other species of *Hypomesus* by its high midlateral scale count, 66 to 73, and the 4 to 7 pyloric caeca; from *H.p. japonicus* by the scale count, the shorter pectoral fin, 41 to 48 per cent of the distance between the pectoral and pelvic insertions.

Description. D (8)9–10; C 19; A (12)13–16; V 8; P 14–16(17); L.L. 4–12; midlateral scales 66–73; vertebrae (62,63)64–68(69,70); gill-rakers 10–13+21–24=31–36; branchiostegals 7–8; pyloric caeca 4–7.

Head 4.7–5.4 in standard length; depth 4.6–7.3 in standard length. Orbit (4.0)4.1–5.9 in head length. Snout length .8–1.1 of interorbital width. Pectoral 41 to 48 per cent of the distance to the pelvic insertion. Longest anal ray 2.6–3.5 times in head length. Postanal length about four times in standard length. Adipose base short, less than orbit diameter.

Small pointed teeth on dentary, maxillary, premaxillary; none of teeth enlarged. Pelvic origin usually behind, sometimes opposite, dorsal origin. Dorsal origin posterior to midpoint of body (to caudal base). Ductus pneumaticus attached to anterior end of gas bladder. Lateral line incomplete, extending less than a head's length along the body.

Peritoneum pale, lightly speckled. Body generally straw coloured, a solid mediolateral band with well-defined edges (obscured by silvering in life). In life, blue-green back, sides silver with purple iridescence.

Largest specimen reported in California 254 mm, in British Columbia 185 mm.

Sexual dimorphism. Small tubercles on scales and fin rays in male, obsolescent in female. Female silver-white and rounded in form; male golden-sided and less full.

Life-history. A marine species, although sometimes entering brackish water. One specimen examined from freshwater—Sandy River, 10 miles east of Portland, Oregon. Spawns from May to October on fine gravel. The eggs stick to the gravel; hatching occurs in ten or more days. The

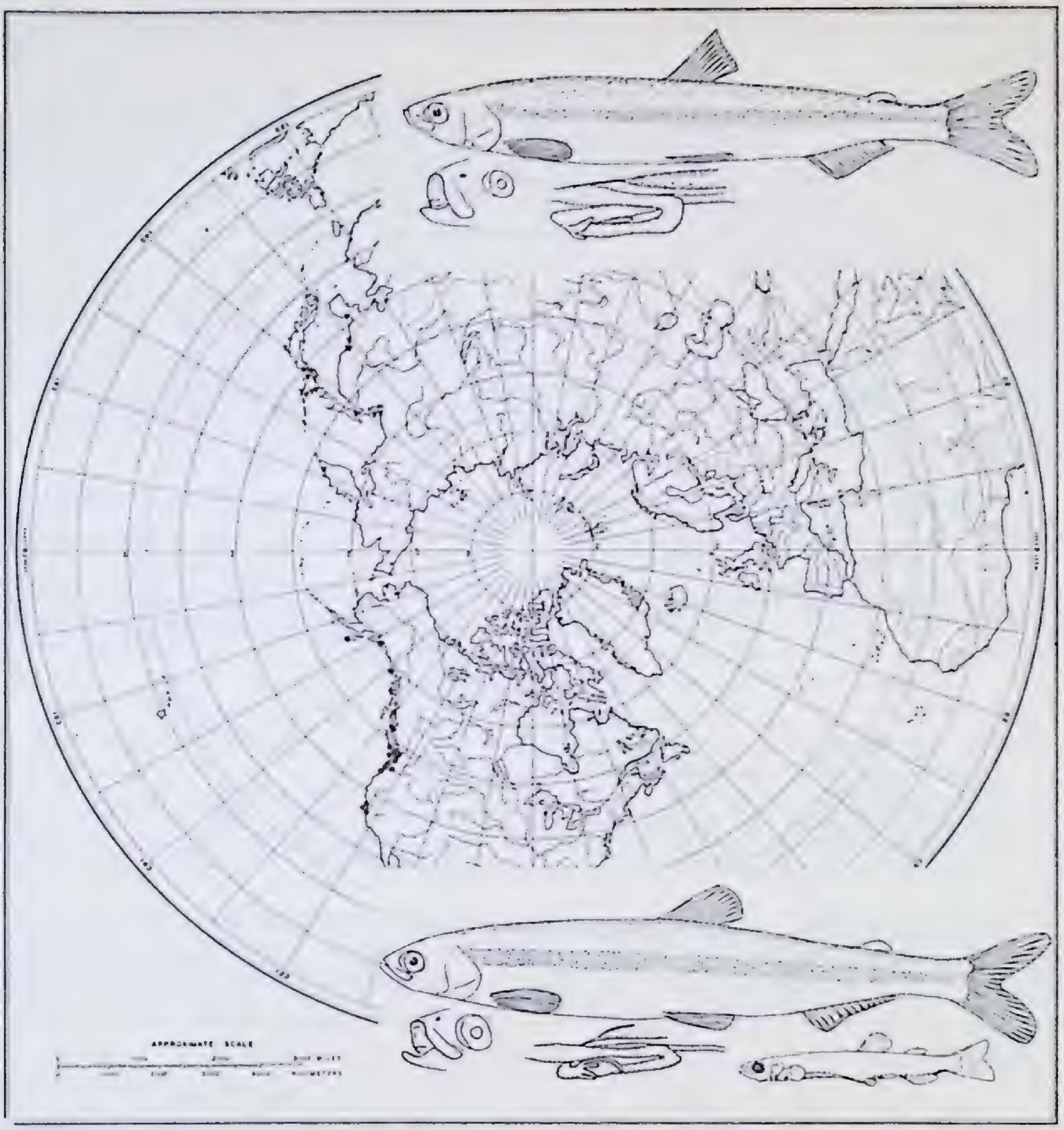

FIGURE 9. Distribution of *Hypomesus p. pretiosus*—circles, and *H. p. japonicus*—triangles. Upper inset shows 143 mm male *H. p. japonicus* (BC60–154), dentition, intestine, gas bladder. Lower inset of 136 mm male *H. p. pretiosus* (BC59-69), dentition, intestine, gas bladder, and 31 mm larva after Follett (1952).

surf smelt may spawn at the age of one and live to the age of three. Usual food crustacea. (For further details, *see* Hart and McHugh (1944), Schaefer (1936), and Yapchionges (1949).)

Systematics. As there has been confusion between this species and *H. olidus,* care must be taken in using the literature. *H. pretiosus* has been thought by some authors to be specifically distinct from *japonicus* (Hubbs, 1925; Hamanda, 1954), but others have regarded them as conspecific (Berg, 1948; Schmidt, 1950; and Andriashev, 1954). As the key indicates, they may readily be separated. But because of slight overlap in characters and because they are allopatric, they are here considered subspecifically distinct.

Material examined. UMMZ128837: one from Sandy River, at Multnomah City, 10 miles east of Portland, Oregon; UMMZ60903: six from San Francisco Bay near Sausalito, California; BC55–371: one from San Juan Island, Washington; BC59–306, BC53–69, BC56–647, BC53–239, BC53–441: 19 specimens from Vancouver, British Columbia; BC55–119: one from Saturna Island, British Columbia; BC53–207: four from Goose Island, British Columbia; BC59–285: one from Barkley Sound, Vancouver Island, British Columbia. The following from the Wilimovsky collection, now in the U.B.C. collection: L58, 1134a: one from Baranof Island, Little Port Walter; K57–90: one from Orca Inlet, Prince William Sound, Alaska; K57–157 and K57–158: two from Port Gravina, Prince William Sound, Alaska.

Range. Known in the eastern Pacific from Prince William Sound, Alaska to Monterey Bay, California.

Hypomesus pretiosus japonicus (Brevoort) **chika** (Japanese) **malorotaya korioshka** (Russian)

Synonymy

Osmerus japonicus Brevoort 1856, p. 278, pl. X, fig. 2 (colour), Hakodate, Japan (*Osmerus olidus* in text, *O. japonicus* on plate).

Osmerus oligodon Kner 1865, p. 9, taf. IV, fig. 1, Dekastri Bay, Russia.

Spirinchus verecundus Jordan and Metz 1913, p. 11, pl. 1, fig. 2, Chinnampo, Korea (holotype 4570 Carnegie Mus., now at Chicago Nat. Hist. Mus.; paratype 4097 Stanford U., *verecundus* auctorum).

Diagnosis. Distinguished from other species of *Hypomesus* by the high number of midlateral scales, usually 63 to 67, and its 4 to 7 pyloric caeca; from *H. p. pretiosus* by its fewer scales, 63 to 67; its shorter pectorals, usually 47 to 55 per cent of the distance between the pectoral and pelvic insertions.

Description. D (8)9–12; C 19; A (11)12–15(16,17); V 8; P (12)13–15(16); L.L. 9–14; midlateral scales (61,62)63–67(68,69); vertebrae (59,60)61–65(66,67); gill-rakers 11–13+20–26=33–36; branchiostegals 8; pyloric caeca 4–8.

Head 4.8 to 5.2 times in standard length; depth 5 to 6 in standard length; orbit 4.2 to 4.7 in head length; adipose base short, less than orbit. Pectoral length usually 47 to 55 per cent (44 to 59 per cent) of distance between insertions of pectoral and pelvic fins. Longest anal ray about 2.6 to 3.3 times in head length. Postanal length about four times in standard length.

Small pointed teeth on dentary, sometimes on maxillary and premaxillary; none of teeth canine. Pelvic origin usually behind dorsal origin. Dorsal origin usually anterior to midpoint of body (to caudal base). Ductus pneumaticus attaches to anterior end of gas bladder. Lateral line incomplete, extending less than a head's length along the body.

Peritoneum light or silver, slightly speckled. Body generally straw coloured. A solid midlateral band with well-defined edges (obscured by silvering in life).

(For distribution and illustration, *see* Figure 9 above).

Hamanda (1954) reports specimens up to 160 mm standard length, Hikita (1952) to 204 mm total length, Berg (1948) to 207 mm total length. This is the largest species of *Hypomesus*.

Life-history. Marine, sometimes in brackish water. Spawns in bays of Hokkaido in May (Hamanda, 1961), on Russian shores in spring (Berg, 1948).

Systematics. As there has been confusion between this species and *H. olidus*, care should be taken in using the literature.

Jordan and Gilbert (1899) and Hubbs (1925) place *Osmerus oligodon* in the synonymy of *Hypomesus olidus;* Berg (1948) in that of *pretiosus*. It is here considered a synonym of *H. p. japonicus*. Although Kner's description gives the midlateral scales as about 60, the excellent figure has 68 scales. Only *H. p. japonicus* has 68 scales. The description differs from *olidus* and agrees with *japonicus* in the length of the adipose base, pectoral length, number of pectoral and anal rays, dorsal and anal length, pelvic insertion, total length, and habitat. The description differs from *H. transpacificus* in the number of anal rays, orbit size, pelvic insertion, and total length (Also *transpacificus* is not known anywhere near the type locale of *oligodon*). Berg (1948, p. 450, footnote) gives a further indication of its identification with *H. pretiosus japonicus*: a specimen of *H. pretiosus* was taken from Dekastri Bay (type locale of *Osmerus oligodon*) which had more than 60 vertebrae, five pyloric caeca, and a pectoral fin with length 51 per cent of distance to pelvic insertion. For these reasons *Osmerus oligodon* Kner is considered a synonym of *H. pretiosus japonicus* Brevoort.

Material examined. BC60–154: one from Shokotsu River, Hokkaido; NMC60–496: 20 from Mori, Japan Sea, Hokkaido; UMMZ145811: one from Avatcha Bay, Kamchatka, USSR, collected by A. Popov 1930. Vertebrae counts in description from Hamanda (1954).

Range. Known in the western Pacific from Wonsan, Korea, to Petropavlovsk, Kamchatka.

Hypomesus olidus (Pallas)
pond smelt
malorotaya korioshka (Russian)
ishikari-wakasagi (Japanese)

Synonymy

Salmo olidus Pallas 1814, p. 391, rivers and lakes of Kamchatka, Kamchatka River; *olictus* auctorum (date established by Opinion 212, Int. Comm. Zool. Nomencl.).
Salmo spirinchus Pallas 1814, p. 387, rivers of Kamchatka (*ex parte*).
Hypomesus olidus bergi Taranetz 1935, p. 85, tundra lake of Tuimi River, 6 km above Nogliki, Sakhalin.
Hypomesus olidus drjagini Taranetz, p. 85, Kolyma River, Siberia.
Hypomesus sakhalinus Hamanda 1957, p. 136, fig. 1–3, Lake Taraika, Sakhalin.

Diagnosis. Distinguished from other *Hypomesus* by the low number of pyloric caeca, 0 to 3; the attachment of the ductus pneumaticus behind the anterior end of the air bladder (discovered by Hamanda, 1957); and the great length of its longest anal ray, 1.8 to 2.3 in head length.

Description. D 7–9; C 19; A 12–16(17,18); V 8; P 10–12(13); L.L. 7–16; midlateral scales 51–60(61,62); vertebrae 52–58; gill-rakers 8–12 +17–22=26–34; branchiostegals 6–7(8); pyloric caeca 0–3(4).

Head 4.0 to 5.0 times in standard length; depth 4.2 to 6.3 in standard length. Orbit 3.3 to 4.9 in head length; snout .7 to 1.1 of interorbital width; pectoral length 40 to 80 per cent of distance between origins of pectorals and pelvics. Longest anal ray 1.8 to 2.3 in head length; postanal length about 3.3 in standard length. Adipose base .9 to 1.2 of orbit.

Small pointed teeth on dentary, maxillary, premaxillary; none of teeth enlarged. Pelvic insertion below or anterior to dorsal origin. Ductus pneumaticus attaches behind anterior end of gas bladder, attaching one-fifth to one-seventh along the length of the gas bladder (character discovered by Hamanda, 1957). Lateral line incomplete, extending less than a head's length along the body.

Peritoneum light, speckled slightly. Body brownish, speckled dorsally particularly along the borders of the scales. A poorly-defined speckled stripe starts on the caudal peduncle and fades anteriorly. Snout and operculum speckled.

The longest specimen examined was 102 mm. Andriashev (1954) reports them up to 140 mm and rarely to 185 mm in the mouth of the Anadyr River. A smaller species than *Hypomesus pretiosus.*

Sexual dimorphism. Tubercles on head, scales and rays of all fins of males; reduced or absent in females. The ventral fins tend to be longer in males, almost reaching anus. The pectoral length varies from 62 to 77 per cent (57–80) in males, 55 to 66 per cent (49–70) in females, of the distance to the insertion of the pelvic fin in Japanese and Alaskan specimens.

Life-history. A completely freshwater species, although perhaps sometimes venturing into brackish water. Dwells in lakes or streams. Spawns from April to March in rivers of Peter the Great Bay (Taranetz, in Berg, 1948), middle or end of April in Hokkaido (Hamanda, 1961). Specimens collected from the Copper River, Alaska, on 8th to 9th of June were ripe. Soin (1947) and Nikolsky (1956) give information on spawning and development in the Amur. Here spawning occurs from the end of April to the beginning of May. The occurrence of this species on Sakhalin and Hokkaido would suggest some tolerance to salt water, although the effluence of the Amur River may have provided a freshwater bridge to the former.

Systematics. As this species has been confused with both of the other species of *Hypomesus,* care should be taken in using the literature.

In 1935 Taranetz named *H. o. bergi* from Sakhalin, distinguishing it on the basis of eye-size, number of pyloric caeca, and number of vertebrae. As these characters are widely overlapped by specimens from elsewhere and as there appear to be no other distinguishing characters, *H. olidus bergi* is considered a synonym of typical *H. olidus.*

In the same paper, Taranetz distinguished another subspecies, *H. o. drjagini,* from the Kolyma River, northern Siberia. This was character-

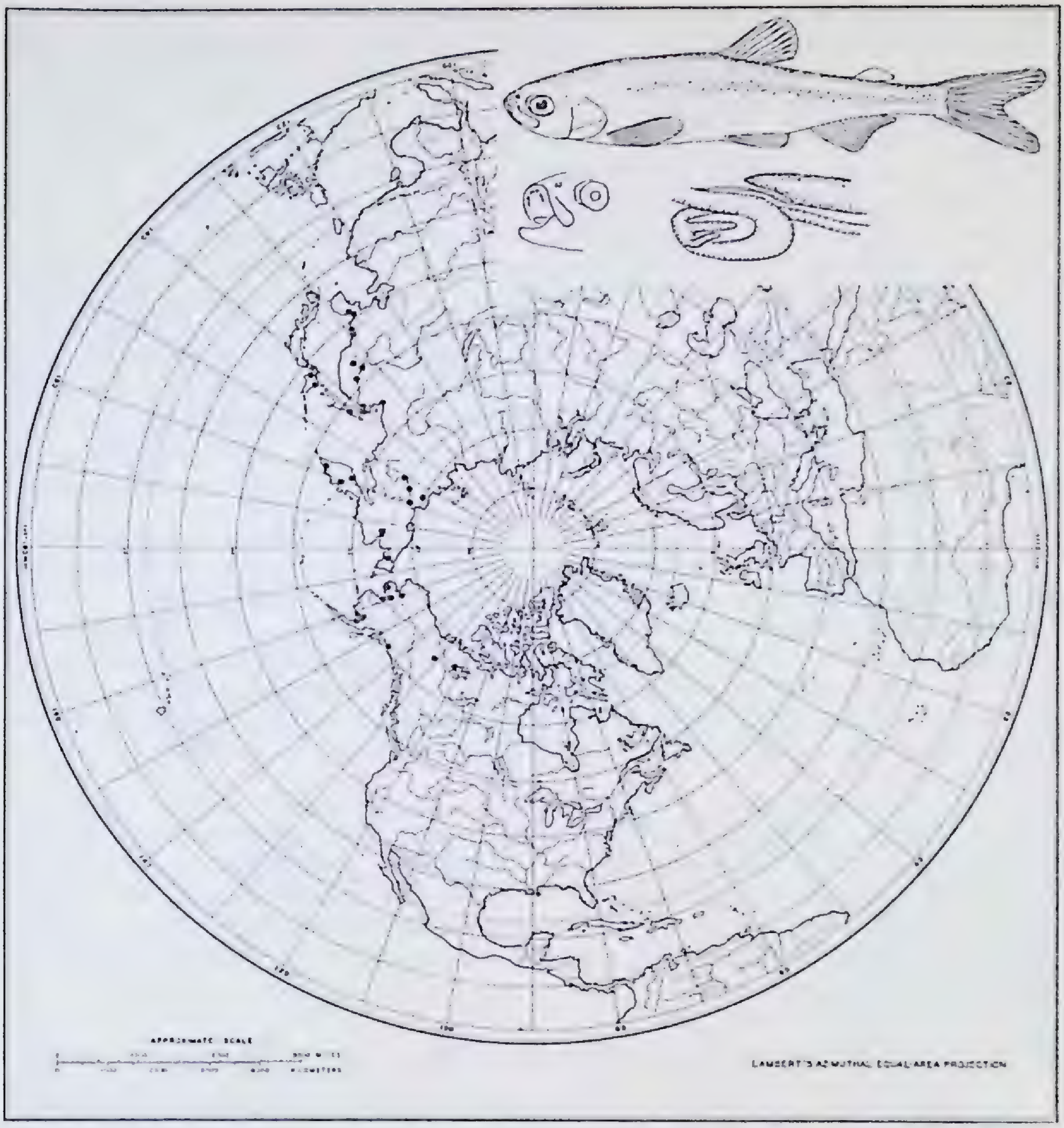

FIGURE 10. Distribution of *Hypomesus olidus*. Inset shows lateral view of 96 mm male (BC60-410), dentition, intestine, and gas bladder.

ized as having pectoral fins 42 to 60 per cent of the distance between the pectoral and pelvic insertions, as contrasted with 61 to 80 per cent in those from Pacific drainages. Further data enable one to see that variation obscures any differences between these drainages. The pectoral length varies: Western Pacific 55 to 85 per cent (Hokkaido 55–77; Sakhalin 63–74; Amur River 62–85; Anadyr Gulf and Kamchatka 56–67); Pacific Alaska 57 to 81 per cent (Copper River 57–73; Nushagak Bay 75–81); Arctic Alaska 55 to 59 per cent (Kobuk River); Arctic Russia 42 to 67 per cent (Lake Krugloe, Kara Gulf 42–59; Kolyma River 53–64; Alazeya River 56–67). Though it is true that Arctic specimens tend to have shorter pectorals (Arctic total variation 42–67, Pacific 55–85 per cent), overlap is so great that it is unwise to designate subspecies on this basis. It may also be noted that *Spirinchus thaleichthys* showed a northward decrease in pectoral length. Since pyloric caeca vary from 0 to 3 in a single population, characterizing subspecies as having two or three is not warranted. The percentages above are from original data: Hamanda (1957), Berg (1948), Taranetz (1935), Walters (1955), and Ivanova (1952).

Ivanova (1952) discovered a relict population of *Hypomesus olidus* in Lake Krugloe, Yamale, Kara Sea drainage. These she named as a new morpha *Hypomesus olidus drjagini* morpha *lacustris*. It does not appear to be even subspecifically different from typical *olidus*, and the infrasubspecific taxon has no status under the International Rules of Zoological Nomenclature. The great hiatus (about 1,700 miles) between Lake Krugloe and the nearest other population, the Alazeya River, Siberia, and the fact that the Kara fauna is of Atlantic affinities are of zoogeographic interest.

In conclusion, there is presently no sound basis for subdivision of *Hypomesus olidus* into subspecies, and it is regarded here as monotypic.

Material examined. NMC60–497: 20 specimens from Lake Ishikari, Furukawa, Hokkaido; BC60–154: four from Shokotsu River, Hokkaido; BC60–409: one from mouth of Naknek River, Alaska; BC60–410: 12 from Snag Point, Nushagak Bay, Alaska. The three following from Wilimovsky's collections now at U.B.C.: 11 from Copper River, Bidabka Bay, Alaska; W57–17: one from 20 miles northwest of Hooper Bay, Bering Sea, Alaska; one from Alaska. ROM14469: three specimens of *Hypomesus olidus* from Good Hope Bay, Smith Arm, Great Bear Lake, N.W.T., Canada.

Range. Known from Wonsan, Korea, in the Pacific, north to Alazeya River, Siberia, including Hokkaido and Sakhalin. An isolated population is known from Lake Krugloe, Yamale, USSR, in the Kara Sea drainage. In North America it is found from Copper River north to Kobuk River, Alaska, and also from the Peel River, Yukon. While this paper was in press, the author collected two young specimens in the Mackenzie River delta at Inuvik, Canada.

Hypomesus transpacificus transpacificus n. sp. **wakasagi** (Japanese)

Diagnosis. Distinguished by the low number of midlateral scales, 54 to 60; the ductus pneumaticus attaching to the anterior end of the gas bladder; and the high number of pyloric caeca, 4 to 5; from *H. t. nipponensis* by the lower number of pectoral (10–12), higher dorsal (9–10) and anal rays (15–17). One or no chromatophores between mandibles.

Description. D 9–10; C 19; V 8; P 10–12; L.L. 8–9; midlateral scales 53–58; vertebrae 53–56; gill-rakers 9–10+19–23=27–33; branchiostegals 7; pyloric caeca 4–5.

Head 4.4 to 4.8 in standard length; depth 4.7 to 5.2 in standard length. Orbit 3.5 to 4.0 in head length; snout length .8 to 1.1 of interorbital width. Pectoral length 58 to 67 per cent of distance between insertions of pectoral and pelvic. Longest anal ray 2.2 to 2.3 in head length. Postanal length 3.6 to 3.8 in standard length. Adipose base short .6 to 1.0 of eye diameter.

Small pointed teeth on dentary, maxillary, premaxillary; none of teeth enlarged. Pelvic origin about opposite dorsal origin. Ductus pneu-

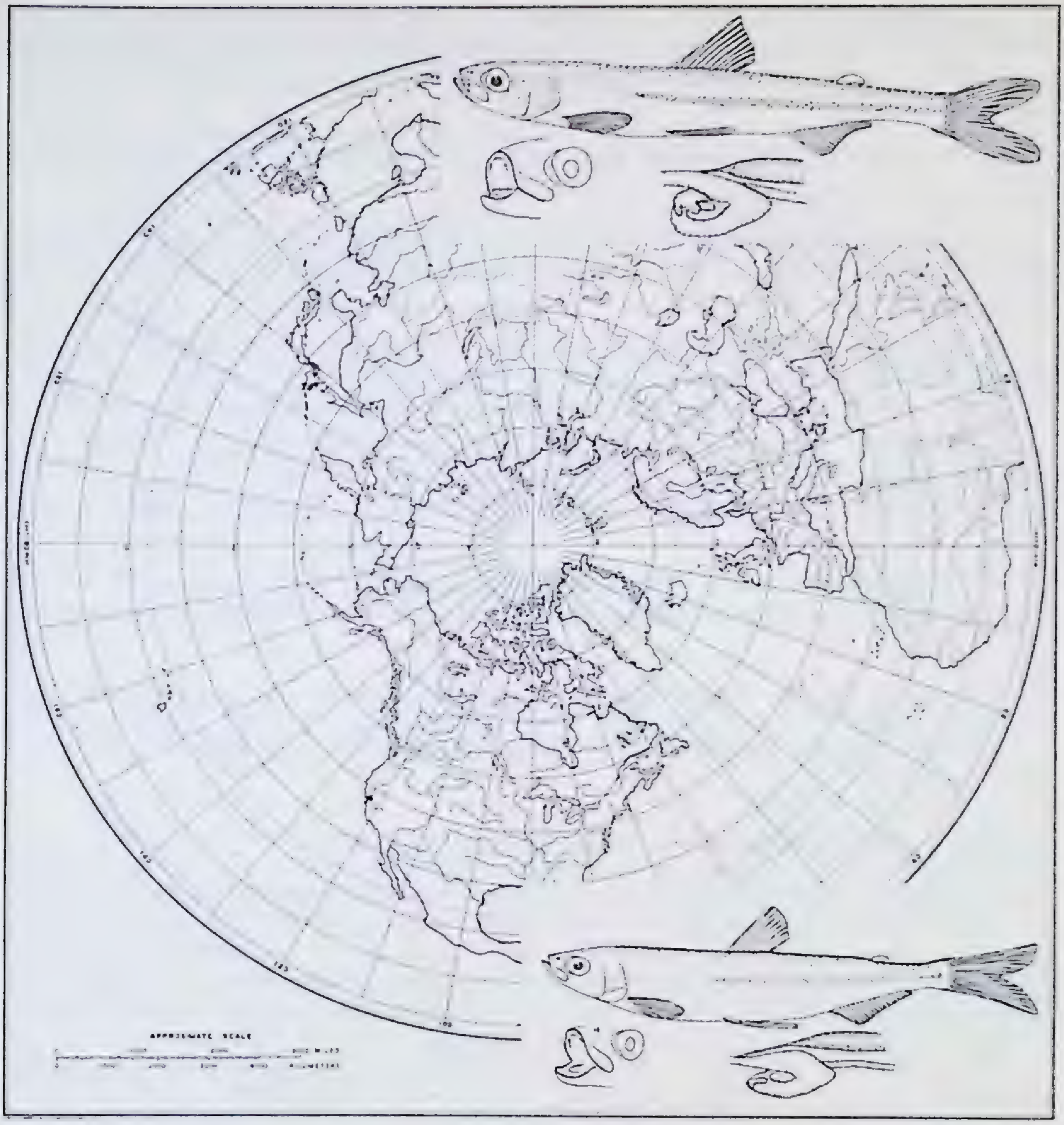

FIGURE 11. Distribution of *Hypomesus t. transpacificus*—circles, of *H. t. nipponensis*—triangles. Upper inset 85 mm male holotype of *H. t. nipponensis*, dentition, intestine, gas bladder. Lower inset 68.6 mm holotype of *H. t. transpacificus*, dentition, intestine, gas bladder.

maticus attached to anterior end of gas bladder. Lateral line incomplete, extending less than a head's length along the body.

Peritoneum pale, lightly speckled. A faintly speckled midlateral band, commencing on the caudal peduncle and fading anteriorly. Usually none, occasionally one chromatophore between mandibles.

Longest specimen reported 98 mm standard length (Erkkila, 1950).

Life-history. Euryhaline. Known in brackish and freshwater portions of the Sacramento – San Joaquin River. Herald (1961) says it spends nearly all its life in the fresh waters of the Sacramento River delta. Erkkila

(1950) reported this species in salinities of from 2 to 157 parts per 100,000 in the lower Sacramento and San Joaquin and their juncture downstream to 4 miles below Antioch. Stomachs contained *Daphnia* and *Neomysis mercedis*.

Taxonomy. This species has been referred to in the literature as *Hypomesus olidus*.

Holotype. NMC60–499: 68.6 mm in standard length. Collected from the lower San Joaquin River between Three Mile Slough and False River, California.

Paratypes. From same collection as holotype, NMC60–500: one specimen 84.7 mm in standard length; ROM21930: one specimen 57.4 mm; BC61–71: eight specimens 38.3 to 67.2 mm; one specimen 62 mm sent to K. Hamanda, Hokkaido; NMC62–166; 32 specimens 36 to 78 mm, San Joaquin River at Pittsburg, Contra Costa Co., Calif.; NMC62–167: 10 specimens 69 to 82 mm, San Joaquin River at Roberts Island, San Joaquin Co., Calif.

Derivation of name. The name *transpacificus* refers to occurrence on both sides of the Pacific and to the friendship of Japanese and Canadian ichthyologists.

Common name. Wakasagi, the Japanese common name for this fish.

Range. Known only in the lower parts of the Sacramento – San Joaquin River, California.

Hypomesus transpacificus nipponensis, n. subsp. wakasagi

Diagnosis. Distinguished by the low number of midlateral scales, 54 to 60; the ductus pneumaticus attaching to the anterior end of the gas bladder; the high number of pyloric caeca, 4 to 7; from *H. t. transpacificus* by the higher number of pectoral rays (12–14), the lower number of dorsal (7–9) and anal rays (13–15), ten or more chromatophores between mandibles.

Description. D 7–9; C 19; A 13–18(19); V 8; P 12–14; L.L. 4–14; midlateral scales 54–60; vertebrae (52)55–58; gill-rakers (8)9–11(12)+(18,19)20–25(26) = (28)29–36(37); branchiostegals 7; pyloric caeca 4–7.

Head 4.0 to 5.1 in standard length; depth 4.9 to 8.2 in standard length; postanal length about 3.5 to 3.7 in standard length. Orbit 3.4 to 4.0 in head length. Longest anal ray about 2.0 to 2.3 in head length. Snout 1.0 to 1.3 of interorbital width. Pectoral 49 to 69 per cent of the distance between origins of the pectoral and pelvic fins. Adipose base short, .6 to .7 of orbit.

Small pointed teeth on dentary, premaxillary, maxillary; none of teeth enlarged. Pelvics inserted below or anterior to dorsal origin. Ductus pneumaticus attached to anterior end of gas bladder. Lateral line incomplete, extending less than half a head's length along the body.

Peritoneum pale, lightly speckled. Body yellow-brown, speckled dorsally especially along scale borders, on snout and opercle. A faintly speckled midlateral band, commencing on caudal peduncle and fading anteriorly. Ten or more chromatophores between mandibles.

Our largest specimen 103 mm in standard length. Hamanda (1961) reports it to 135 mm standard length, Hikita (1952) to 132 mm standard length. A smaller species than *Hypomesus pretiosus.*

Sexual dimorphism. Tubercles on scales, head, fin rays of males; lacking in females. Pectoral and pelvic fins longer in male.

Life-history. Hamanda (1961) presents a detailed study of the life-history. There are two types of life-history, one an anadromous type and one a completely freshwater. The freshwater type lives in lakes which may or may not have access to the sea (residual or landlocked). Spawning of both types occurs in rivers or on shores of lakes in April or May. Maturity is attained in a year. The anadromous type dies after spawning, while the freshwater type may live up to four years.

Systematics. This form has hitherto been referred to in the literature as *H. olidus.* Although some real records of *olidus* have resided under that name, most records refer to *H. t. nipponensis.* In Hamanda's (1961) study, *sakhalinus=olidus* and *olidus=t. nipponensis. H. olidus* and *t. nipponensis* are sympatric in Lake Ishikari at Furukawa, Hokkaido, and retain their morphological characteristics; hence they must be judged good species.

Holotype. NMC60–498–A: 85 mm in standard length. Collected in Lake Onuma, southern Hokkaido, by K. Hamanda (introduced into this lake from Lake Akan, Hokkaido, according to Tatsuji Ueno).

Paratypes. From same collection as holotype, NMC60–498: 52 specimens 45 to 78 mm in standard length; BC61–28: 10 specimens 49 to 64 mm; ROM21391: 63 mm; three specimens returned to K. Hamanda; BC59–653: six specimens from southern Japan 67 to 103 mm. Vertebrae counts of description from Hamanda (1954) in part.

Range. Known in and around Hokkaido, Japan. Introduced in Honshu and Kyushu. There appear to be native populations in Honshu; these were not plotted on the map because of the difficulty of separating natural and planted populations.

Genus **Mallotus** Cuvier

Synonymy

Mallotus Cuvier 1829, p. 305 (type species: *Salmo groenlandicus* Bloch = *Clupea villosa* Müller, by monotypy).

Vomerine teeth small, in arch across vomer. Palatine teeth all small. Maxillary extends to about midpoint of pupil. No striae on opercle or subopercle. Distance from snout to dorsal origin greater than from dorsal origin to caudal base. Midlateral ridge, anal shelf, and elongate midlateral scales in male. Gill-rakers 33 to 44(48). Pyloric caeca 4 to 9. Stomach with blind sac. Lower jaw spatulate. Anal rays 16 to 23, pectoral 16 to 21. Lateral line scales 170 to 220, lateral line complete. Adipose base large, exceeds diameter of orbit. Orbit diameter one to two times in depth of caudal peduncle.

Proethmoids fused. No mesethmoid ossifications. Parietals separated by the supraoccipital posteriorly. Pterosphenoid not reaching parasphenoid anteriorly. A slit between hyomandibular and preopercular. Fourth actinost doubly bifid so there appear to be six actinosts (osteological characters from Chapman, 1941).

One species: *Mallotus villosus*, circumpolar marine in Arctic, Pacific, and Atlantic.

Mallotus villosus (Müller)

capelin
le capelan (French)
lodde (German, Norwegian, Dutch)
villakuore (Finnish)
karafuto-shishamo (Japanese)

Synonymy

Clupea villosa Müller 1776, p. 50, Islandos (= Iceland; ex Olafsen).
Salmo arcticus Fabricius 1780, p. 177, Greenland; (not of Lacépède 1804).
Salmo catervarius Pennant 1784[1], p. cxxvii, Bering Island, Avatcha Bay, mouth Kamchatka River (ex Steller MS., via Pallas).
Salmo groenlandicus Bloch 1793, p. 99, pl. 381, fig. 1, Greenland.
Salmo lodde Lacépède 1804, p. 156, 219, Greenland, Iceland, Norway, Newfoundland (ex vernacular, Bonnaterre).
Clupea lodna Hermann 1804, p. 316, Iceland (ex Olafsen and Polvelsen 1772).
Salmo socialis Pallas 1814, p. 389, tab. LXXXI, fig. 2, islands between Asia and America (date established by Opinion 212 Int. Comm. Zool. Nomencl.).
Osmerus microdon Valenciennes 1848, in Cuvier and Valenciennes, p. 385; 392, tab. 621, no locality.
Mallotus elongatus Mori 1930, p. 5, fig., mouth Tumen River, Keiko, Korea.
Sudis squamosa Chapman 1939, p. 519, off southern shore Alaskan Peninsula. (holotype: U.S. Nat. Mus. 108150).
[*Mallotus villosus catervarius* natio *schultzi* and natio *catervarius* Rumjanzen 1947, p. 48, have no status under the rules of the Int. Comm. Zool. Nomencl.]

Diagnosis. Distinguished from all other osmerids by the high number of scales along the lateral line, 170 to 220, from all other except *Thaleichthys* by the numerous pectoral rays (16)17 to 21, from all other except *Hypomesus olidus* by the long adipose base, 1.5 or more times orbit; from all other by the small ninth pelvic ray.

Description. D 10–14; C 19; A (16)17–22(23); V 8i; P (16)17–20 (21); L.L. 170–220, above 15–23, below 14–22; vertebrae (62,63)64–72(73); gill-rakers 8–13+24–33(35)=33–44(48); branchiostegals 8–10; pyloric caeca (4)5–8(9).

Head 3.9 to 5.0 times in standard length; depth 4.9 to 8.3 times in standard length. Pectoral fin extending one-third to two-thirds the distance to pelvic origin. Adipose base long, exceeding 1.5 times diameter of orbit. Adipose subrectangular rather than oval. Pelvic insertion anterior or under dorsal origin.

Small pointed teeth on dentary, premaxillary, maxillary; none enlarged. Gill-rakers slender, length about two-thirds of orbit diameter. Lateral line complete.

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[1] Berg considers this work non-binomial, contrary to Schultz (1937) and Hubbs and Chapman (1951). This question has bearing on the names of the round whitefish and the trout-perch.

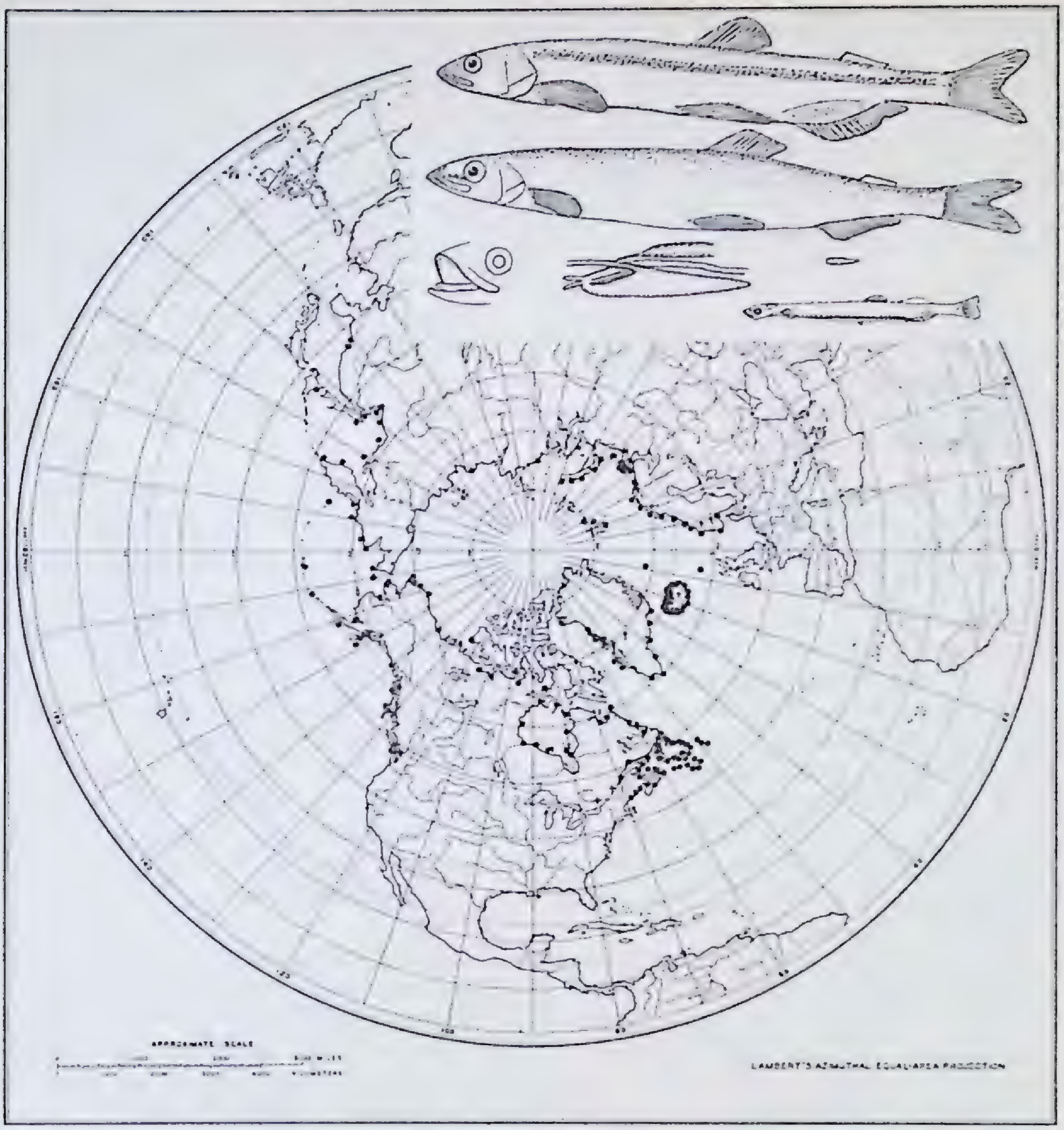

FIGURE 12. Distribution of *Mallotus villosus,* circles—recent, crosses—fossil. Inset shows, above, 121 mm male; below, 123 mm female (NMC60–471), dentition, intestine, gas bladder, elongate male midlateral scale, and 29 mm larva (the latter after Templeman, 1948).

Peritoneum silver overlain with such dense speckling as to be almost black. Dusty olivaceous above, silver-grey sides, opercles punctate.

Sleggs (1933) gives the length to 202 mm for Newfoundland specimens; Herschel Island specimens were found to range from 110 to 156 mm fork length in a spawning population by J. G. Hunter and the author. Andriashev (1954) gives the total length to 220 mm for the Pacific form.

Sexual dimorphism. The males have a prominent midlateral ridge formed by the elongation of the rows of scales immediately above the lateral line and the swelling of the musculature. The females are smoothsided. The pectoral, dorsal, and anal fins of the male are enlarged and fan-like. The first 10 to 12 anal rays are thickened. The body above the anal fin projects outward like a shelf in the male. The male snout is blunter. Small conical tubercles form on the head, the inner surface of the pectoral rays, the lower caudal rays, and the lower portion of the body in the male; absent in the female. The female is more slender. Sexual dimorphism is so prominent that sexes may be recognized in fossils (*See* figure for differences).

Life-history. A completely marine species. Spawns from April to October. Eggs are laid on fine gravel or sand on beaches, or on banks at depth of 40 to 80 metres (Pitt, 1958), at temperatures from 2.8° to 5°C. Hatching takes place in two or three weeks. Templeman (1948), Hart and McHugh (1944), and Pitt (1958, 1958*a*) give further details of life-history and growth.

Systematics. In 1937, Schultz compared the capelin of the North Pacific and North Atlantic. He was able to separate Atlantic from Pacific specimens using a character index (the dorsal rays + anal + pectoral + number of scales below the lateral line—the total number of gill-rakers on the first arch). He therefore concluded that the Atlantic and Pacific forms were separate species; the name *Mallotus catervarius* (Pennant) was revived for the Pacific form, and the name *M. villosus* (Müller) was retained for the Atlantic form. Some later authors, such as Berg (1948), Schmidt (1950), Andriashev (1954), and Wilimovsky (1954), have not followed Schultz in distinguishing these forms as species, usually recognizing them at the subspecific level. Schmidt (1950) did not believe species could be recognized on such a "statistical basis." This author considers a character index adequate if all the specimens can be separated and if the forms are sympatric; if the forms are allopatric, such separation is not deemed sufficient.

Examination of further material, including Arctic specimens, gives evidence that the Atlantic and Pacific capelin are consubspecific. As shown on the distributional map, capelin are continuous across the Canadian Arctic (*see* map) and the Russian Arctic, except for the hiatus from Bering Strait to the Lena delta. This hiatus may be an artifact due to incomplete collecting. Andriashev (1954, p. 116) admits there is only scrappy knowledge on the distribution of this species in Arctic waters. Schultz (1937) did not examine Arctic specimens. In this study, Herschel Island, Yukon, specimens were found to range from 27 to 35 in their character index; Hudson Bay, Manitoba, from 29 to 35; Coppermine, Northwest Territories, 23. Thus Arctic populations are intermediate between the values given by Schultz for Pacific (22–28) and Atlantic (30–38) forms. Because of the probable Arctic populations, at least across Canada, and the intermediacy of Arctic specimens, *Mallotus villosus* is regarded as a monotypic species.[1] The differences that Schultz correctly pointed out can be regarded as clinal. The character index is high in the Atlantic, intermediate in the Arctic, and low in the Pacific. The cline probably arose by differentiation of Atlantic and Pacific populations separated by southward depression of isotherms and/or the Bering land bridge during the

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[1] While this paper was in press, D. V. Ellis has published the same opinion in the latest issue of *Arctic.*

Wisconsin glaciation. Diffusion of characters probably took place during the subsequent mixing, perhaps first in the hypsithermal period, following deglaciation.

Vladykov (1941) has also noticed a difference between Atlantic and Pacific capelin. In the males the anal rays are fused distally into a plate (lamina pinnae ani). Different numbers of rays are fused into this lamina in the two oceans. However, the difference is hardly of subspecific note; even the modal count is the same. The following data are from Vladykov (1941).

Percentage number of fused rays

	4	5	6
Pacific	11.5	66	13.5
Atlantic	38	54	5

Fossils. Pleistocene or post-Pleistocene fossils of *Mallotus* are well known (*see* distribution map: Canada, Greenland, Iceland, Norway, and Yugoslavia). Agassiz's (1843) description and figure of fossil capelin from Greenland and Bolkay's (1925) from Bosnia show no characters different from recent specimens. A series of fossil capelins from the Green Creek area, Ottawa, Canada, from the National Museum (now in the Institute of Fisheries, U.B.C.) were examined. Meristic characters were not different from those of modern capelin: D 10–11; A 16–18; V 8–9; P 15–20; abdominal vertebrae 36–38, caudal 23–27, total 66. The slight decrease in the number of parts may be attributed to their being obscured or lost in fossilization. However, counts are still within the range of present material. Most of the specimens could be recognized as males by the sexual dimorphism of the fins. Though most of the fossils are not outside of their present range, the one reported in Bosnia by Bolkay (1925) is. It is positive evidence for a boreal or subarctic climate in the Mediterranean during glaciation. (For further information on fossils, *see* Ami (1901), Bolkay (1925), Jensen (1948), Dawson (1894), Andrée (1920), Richardson (1870), Agassiz (1843, 1848), Sars (1865), and Collett (1877)).

Material examined. BC58–435: three from near Point Roberts, southern British Columbia; BC53–28: one from Departure Bay, Vancouver Island, B.C.; BC56–519: three from Vancouver, B.C.; BC58–220: one from Marmot Bay, Kodiak Island, Alaska; Wilimovsky collection now at U.B.C., John Cobb Station 43–13: two from Chukchi Sea at 67° 13.5′ N., 166° 23′ W., and three from Station 43–57 Chukchi Sea at 69° 17.2′ N., 166° 53′ W.; BC58–152: five from Hudson Bay, Manitoba; BC59–349: one from near Coppermine River, Northwest Territories; BC56–319; three, Bras d'Or Lake, N.S.; NMC60–471: 11, Herschel Island, Yukon Territory (these 11 donated to U.B.C.).

Range. In the Pacific south to the Strait of Juan de Fuca, Washington, and Tumen River, Korea; in the Atlantic south to Penobscot River, Maine, and Oslo, Norway. Found north around the mainland of Canada, Alaska, and Russia. Also from southern tip of Greenland northward to Thule and Scoresby Sound around Iceland, the Faeroes, Jan Mayen, Spitsbergen, and western Novaya Zemlya.

FORMS EXCLUDED FROM THE OSMERIDAE

The following, which have at various times been placed in Osmeridae, are excluded from that family:

Eperlanus chinensis Basilewski 1855 belongs to the family Salangidae according to Mori (1952).

Therobromus callorhini Lucas 1899, in Jordan and Gilbert, named from bones in fur seal stomachs, was shown by Chapman (1941) not to be an osmerid.

Salmo inhaghitsh Walbaum 1792 (ex Pennant) was questionably placed in the synonymy of *Hypomesus pretiosus* by Berg (1948). The number of pelvic rays, 10, exclude it from Osmeridae which have eight. The habit (=form) of a carp and very large scales also exclude it from Osmeridae. Pennant assigned it to the Coregonini, which placement is probably correct.

Osmerus cordieri Agassiz (1843), a fossil, is excluded from the Osmeridae on the basis of too few vertebrae, 38 to 40, rather than 55 to 70.

Osmerus glarisianus Agassiz (1843) is similarly excluded from Osmeridae, having about 40 vertebrae. This and the above species are placed in Scopelidae by Woodward.

Osmerus hebridicus Yarrell 1838 is a synonym of *Argentina sphyraena*, according to Cohen (1958).

The several fossil species of *Osmerus* named from the Upper Miocene of Italy may be excluded from Osmeridae by, among other characters, the number of vertebrae. These fossil species are as follows: *O. albyi*, *O. larteti*, *O. propterygius*, and *O. stilpnos* of Sauvage 1873; *O. scarabellii* of Bonomi 1896; *O. d'achiardi* of Bosniaski, which is a *nomen nudum* (*fide* Woodward, 1901).

Osmerus sp. indet. of Eastman 1917, a fossil from the Oligocene or lower Miocene of Montana, is excluded from the Osmeridae on the basis of having too few vertebrae, only about 30.

Osmerus albidus of Lacépède, 1803, is a Synodontid.

Osmerus lemniscatus of Lacépède, 1803, is a Synodontid.

THE EVOLUTION OF THE OSMERIDAE

The centre of origin, judging from Figure 13, would seem to have been in the Pacific, as all the species and genera are found in the Pacific and its drainages. With similar reasoning, the eastern Pacific (eight species and subspecies) would seem more likely to have been the centre of origin than the western Pacific (six species and subspecies). However, this reasoning makes three assumptions. First, that species stay in their place of origin; secondly, that a species arising in one ocean does not radiate on entering another ocean; lastly, that there has not been extinction of several species in one ocean. As an example of the last, Ekman (1953) gives a list of the molluscs of the late Tertiary then found in the Atlantic but now only in the Pacific. He also says that poverty of the North Atlantic is due to climatic deterioration. Existing fossils are of little help in determining where the osmerids originated. The only known fossils are Atlantic Pleistocene. The relatively young age of these does not enable us to make statements on where the osmerids originated. Thus, although it seems a little more likely that osmerids originated in the Pacific, there is no certainty in this theory (hence the main osmerid stem is not indicated in Figure 13 in any ocean).

Although the place of origin of the Osmeridae cannot yet be determined, it does seem quite likely that most of the present genera evolved in the Pacific. Their richness and endemism indicate this. That their recent evolution has been in the Pacific is bolstered by the presence of several pairs of subspecies endemic to the Pacific, which have presumably recently evolved there. Forms in the Arctic and Atlantic oceans can readily be derived from the Pacific, as has been demonstrated with *Mallotus* and *Osmerus*.

As may be seen from the distribution maps and from Figure 13, there are several pairs of related taxons which have an amphi-Pacific distribution. These are—

WESTERN PACIFIC	EASTERN PACIFIC
Spirinchus lanceolatus	*Spirinchus thaleichthys*
Hypomesus pretiosus japonicus	*Hypomesus pretiosus pretiosus*
Hypomesus transpacificus nipponensis	*Hypomesus transpacificus transpacificus*

Andriashev (1939) discusses other examples of amphi-Pacific distribution. Each of these geminate pairs is absent from the northern perimeter of the Pacific Ocean. This enables one to establish a theory on their mode of origin, a *reciprocating isolation mechanism.* The following sequence is visualized in this theory. One commences with a taxon found on one side of the Pacific. Being warm stenohaline, it is absent from the northern perimeter of the Pacific. The ocean gap below this cool region in the northern perimeter is too large to permit larvae to drift across. The adults being *litophilus* (new term meaning coast-loving, 0 to 200 metres over the Continental Shelf) avoid pelagic ocean waters. When climatic warming occurs, the form is free to cross to the other side, either along the Aleutian-Kommandorskie Island series or across the narrow Bering Strait. Distribution thus becomes continuous around the northern perimeter of the Pacific. Climatic cooling then results in southward depression and consequent separation into two populations, one on each side. Following isolation, speciation or subspeciation may take place. Thus there is a reciprocating isolation mechanism, following climatic cycles, which is capable of inducing speciation. This mechanism applies only to species that live in the sea for at least part of their lives. That there have been several reciprocations is evidenced by the different taxonomic levels of the pairs—subspecific, specific, and in the case of certain Embiotocidae (Tarp, 1952), generic.

Among other factors the inability of freshwater fishes to move as readily as marine fishes latitudinally might account for the relative paucity of species of freshwater smelt. The difficulty of headwater capture and the transient existence of the Bering land bridge combine to prevent freshwater forms from using the reciprocating isolating mechanism and speciating as frequently as marine and anadromous forms.

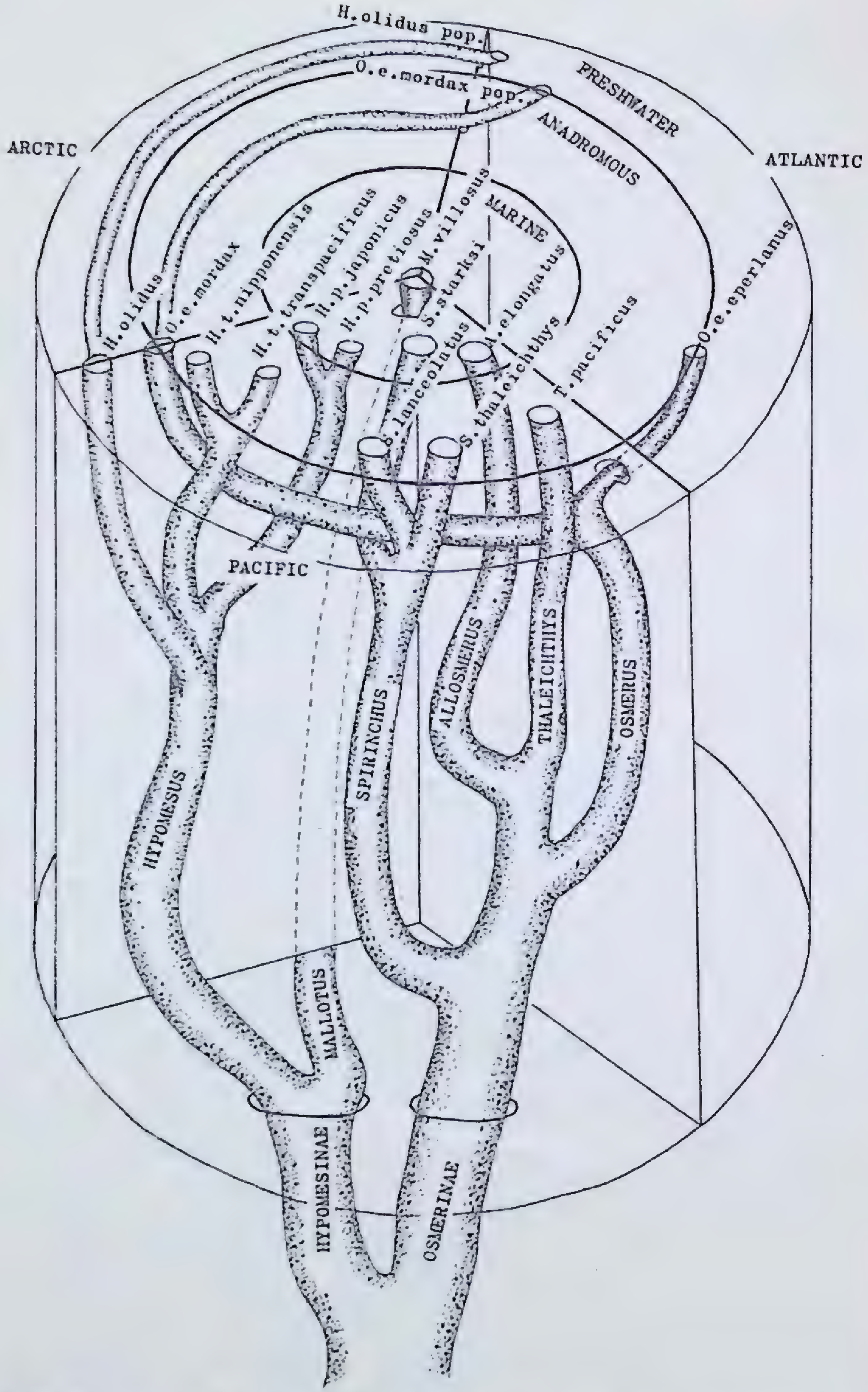
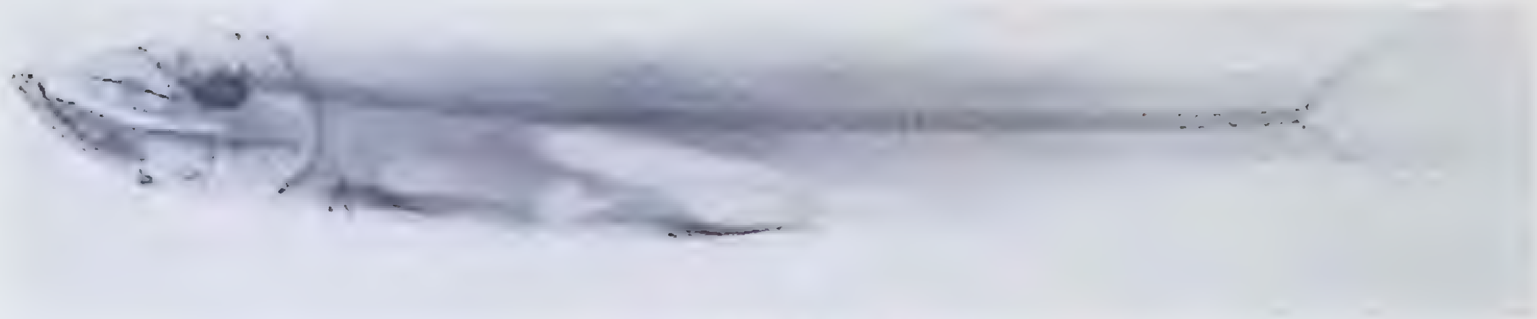
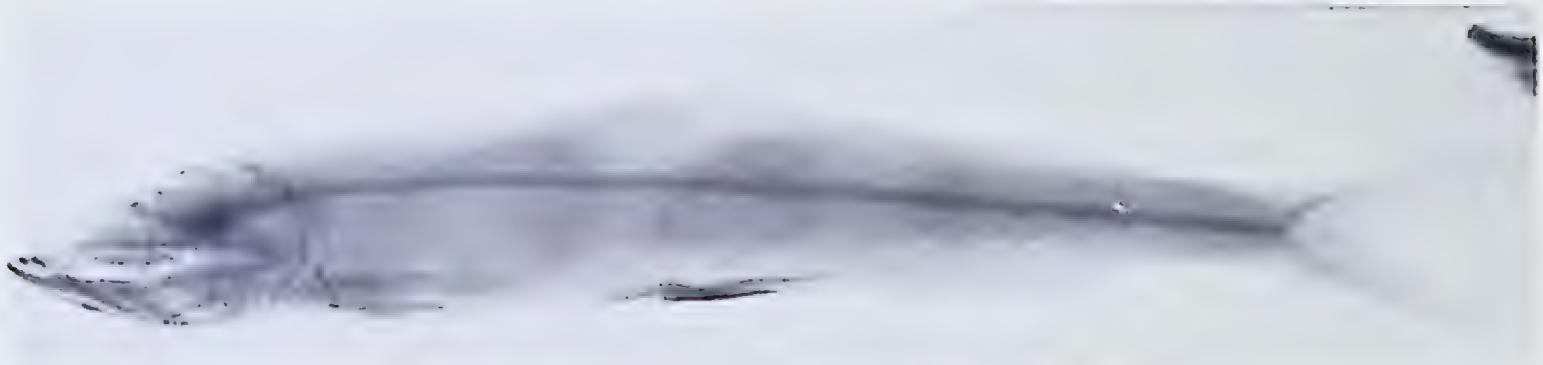


Figure 13. The geographical and ecological evolution of the Osmeridae, evolving into different ways of life—freshwater, anadromous, and marine, and into different oceans—Pacific, Arctic, and Atlantic. *Osmerus* enters the Atlantic by way of Arctic Canada and Arctic Russia.

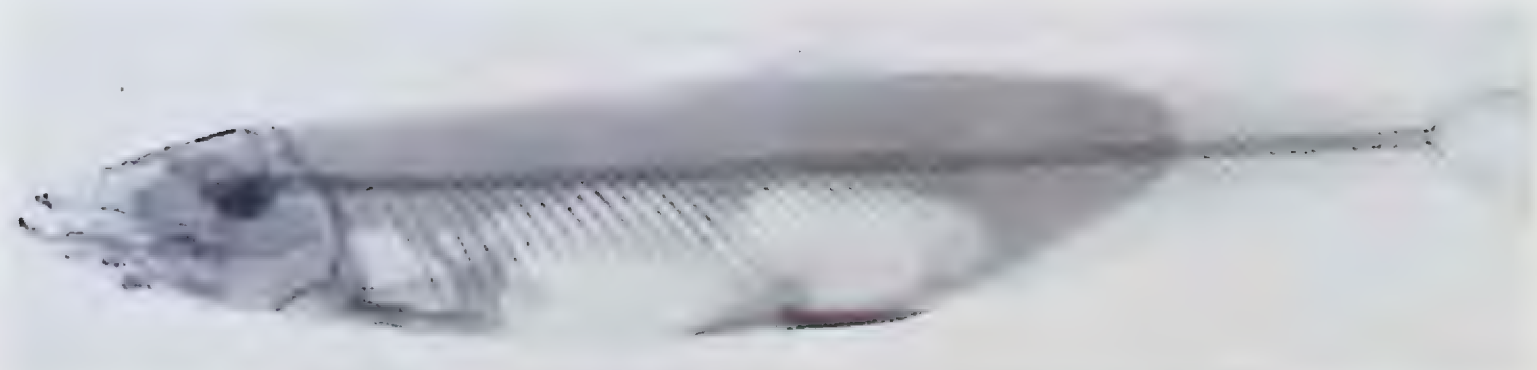


Spirinchus starksi—CAS25470



Osmerus eperlanus mordax—NMC59-322-A

Thaleichthys pacificus—BC60-450



Hypomesus transpacificus transpacificus—NMC60-500

FIGURE 14. X-rays showing the axial skeleton of four species of smelt.

It may be noted, aside, that there are barriers to such an isolating mechanism working in the Atlantic. First, there are greater gaps between land masses, three major gaps instead of one. Secondly, there exist temperature-current barriers such as the Labrador Current. With regard to the former it is true that the Wyville-Thompson ridge provides a bridge from England–the Faeroes–Iceland–Greenland, but it still fails to bridge the Canada-Greenland gap and, moreover, is at some depth, at least at the present sea-level. Thus the more stringent requirements militate numerous species resulting from the reciprocating isolation mechanism in the North Atlantic.

The southern limits of the smelt family[1] are closely related to the southern limits of the boreal zone as depicted by Hedgpeth (1957). The major exception to it is in eastern Asia where the boreal zone includes the Yellow Sea, whereas the smelts do not descend further south than the Japan Sea. The northern limits of the family are marked by the distribution of *Osmerus* and *Mallotus*, the latter being most northern. The northern limits of the family agree closely with Dunbar's (1954) subarctic zone, with the exception that there are a few records along the continental coast of Canada and Russia in his arctic zone. Only the species that can tolerate subarctic conditions are known from the Atlantic. The smelt family can be described as a boreal-subarctic family.

There is another interesting phenomenon that can be observed by examination of the phylogenetic tree in Figure 13. There appears to be a tendency to invade and fill both anadromous and marine niches. The *Hypomesus*, the *Spirinchus*, and the *Allosmerus-Thaleichthys* stems, all send shoots into anadromous and marine ways of life. There are six marine and five anadromous species and subspecies in the North Pacific, almost an equal number. There are two possible factors involved. First, ecological diversification avoids competition for spawning grounds and food of young. Secondly, it helps provide reproductive isolation between species. Stated less teleologically, there is more likelihood of two sympatric species surviving and remaining distinct if they utilize different niches because there is less competition and because it provides an effective isolating mechanism. Thus, ecologically diverse species tend to survive. And the evolution of anadromous and marine fishes from one another, having occurred several times in the family, does not appear difficult.

Finally, it must be pointed out that this phylogenetic tree is based only upon the morphology of present-day species. Such a tree must be regarded as provisional until fossil evidence is obtained.

SUMMARY

A three-dimensional dendrogram of the Osmeridae evolving chronologically, geographically, and ecologically is presented. The mode of evolution, including a reciprocating isolating mechanism in the North Pacific is suggested. The relationship of the Osmeridae to other salmonoid families is depicted. The term litophilus or shore-loving is introduced.

Two subfamilies, Hypomesinae (*Hypomesus, Mallotus*) and Osmerinae (*Spirinchus, Osmerus, Thaleichthys, Allosmerus*) are established. Keys,

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[1] The southern limits of the family are Pt. Arguello in the East Pacific; Wonsan, Korea, in the West Pacific; the Loire River, France, in the East Atlantic; the Delaware River, Pennsylvania, in the West Atlantic.

synonymies, descriptions, and spot distribution maps are presented for the 6 genera, 10 species, and 13 species and subspecies. *Spirinchus dilatus* is synonymized with *S. thaleichthys*. *Osmerus eperlanus* is divided into the subspecies *O. e. eperlanus* and *O. e. mordax* (*dentex* being synonymized with the latter). *Hypomesus verecundus* is synonymized with *H. japonicus*, which, in turn, is reduced to a subspecies of *H. pretiosus*. *H. sakhalinus* is synonymized with *H. olidus*, which is considered a monotypic species. A new species and subspecies are named: *Hypomesus t. transpacificus* (California) and *H. t. nipponensis* (Hokkaido). There are thus three species of *Hypomesus: pretiosus, olidus*, and *transpacificus*. *Mallotus catervarius* is considered a synonym of the monotypic circumpolar species *M. villosus*.

RÉSUMÉ

La présente publication est une mise à jour de la taxonomie des éperlans ou Osmëridés du monde entier et une étude de leur évolution. L'auteur y expose des synonymies et il donne des descriptions et des clés des sous-embranchements, des genres, des espèces et des sous-espèces. Des chiffres et des cartes de répartition et de localisation correspondent à chaque espèce ou sous-espèce. Quelques radiographies illustrent la structure de certaines formes.

L'auteur propose deux sous-familles, soit les Osmérinés comprenant les *Thaleichthys*, les *Osmerus*, les *Spirinchus* et les *Allosmerus*, d'une part, et les Hypomésinés comprenant les *Hypomesus* et les *Mallotus*, d'autre part. Le genre *Osmerus* n'est plus constitué que d'une seule espèce comprenant deux sous-espèces: *Osmerus e. eperlanus* de l'Europe et *O. e. mordax* de l'ouest de l'Atlantique, de l'Arctique et du Pacifique. *Spirinchus dilatus* devient synonyme de *Spirinchus thaleichthys*. *Hypomesus verecundus* devient synonyme de *H. japonicus* qui, à son tour, se réduit à une sous-espèce de *H. pretiosus*. *H. sakhalinus* devient synonyme de *H. olidus* qui est considéré comme une espèce monotypique. Une nouvelle espèce comprenant une sous-espèce, jusqu'ici classée comme étant *H. olidus*, devient *Hypomesus transpacificus transpacificus* de Californie et *H. t. nipponensis* d'Hokkaido. *Mallotus catervarius* est considéré comme étant un synomyme de l'espèce circompolaire monotypique *M. villosus*. Ces changements réduisent à six (6) le nombre de genres; à dix (10) le nombre d'espèces; et à treize (13) le nombre d'espèces monotypiques et sous-espèces de cette famille.

Quant à son évolution, elle est fondée sur la morphologie d'espèces récentes, vu que les seuls éperlans fossiles connus (*Mallotus villosus*) sont identiques aux formes actuelles. L'évolution chronologique, géographique et écologique des Osmëridés est schématisée sous forme d'un dendrogramme à trois dimensions. L'auteur propose un mode d'évolution qu'il appelle le mécanisme d'isolement alternatif, comme explication de l'origine des espèces Osmëridés et d'autres groupes en différentes espèces dans le Pacifique-Nord. Enfin, l'auteur traite de la relation entre les Osmëridés et d'autres salmonidés.

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